

INSECTES SOCIAUX

BULLETIN DE L'UNION INTERNATIONALE POUR L'ÉTUDE DES INSECTES SOCIAUX



COMITÉ DE RÉDACTION

J. D. CARTHY, P. H. CHRISTENSEN, K. GÖSSWALD, P.-P. GRASSÉ,
C. JUCCI, A. RAIGNIER, T. C. SCHNEIRLA, T. UCHIDA

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SOMMAIRE

Mémoires Originaux.

Ecological notes on <i>Formica subnitens</i> Creighton (Hymenoptera : Formicidæ), by Gordon L. AYRE	173
The growth and development of colonies of the ant <i>Myrmica</i> , by M. V. BRIAN	177
Serial organization of brood in <i>Myrmica</i> , by M. V. BRIAN	191
The process of queen supersedure in colonies of honeybees (<i>Apis mellifera</i> Linn.), by C. G. BUTLER	211
Zuckerabbau unter der Einwirkung der invertierenden Fermente in Pharynx- drüsen und mitteldarm der Honigbiene (<i>Apis mellifica</i> L.). 1. Sommerbienen der Krainer- und Nigrarasse, von A. MAURIZIO	225
Bumblebee ecology in relation to the pollination of alfalfa and red clover, by J. T. MEDLER	245
Taxonomic status of <i>Formica subnitens</i> Creighton and <i>F. integroides</i> Emery, with a description of the sexuals of <i>F. subnitens</i> (Hymenoptera : Formicidæ), by C. D. F. MILLER	253
A comparison of species and genera in the ant subfamily Dorylinæ with respect to functional pattern, by T. C. SCHNEIRLA	259
Ueber sekundäre Geschlechtsmerkmale bei einigen Ameisenlarven, von P. Chr. TRABERT	299
Beiträge zur Analyse der Bientänze (Teil I), von Wolfgang STECHE	305

Nouvelles de l'Union.

Réunion de la section française	319
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MÉMOIRES ORIGINAUX

ECOLOGICAL NOTES ON *FORMICA SUBNITENS* CREIGHTON (HYMENOPTERA: FORMICIDÆ) (1)

by

Gordon L. AYRE

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Three colonies of the chrysomelid *Chrysolina gemellata* (Rossi) were imported into and released in British Columbia in 1951 in an attempt to control common St. John's-wort, *Hypericum perforatum* L. In one of the areas where it was released, *C. gemellata*, though established, did not increase in numbers. A suggested cause of this was the presence of a large population of the predacious ant *Formica subnitens* Creighton. As a result an investigation of the life-history, food consumption, and activities of this ant was initiated. The following ecological data were obtained during two years of laboratory and field studies.

The area of the studies, a 10-acre field, was approximately five miles north of Westbank. The field reportedly had been cleared 25 years previously and then abandoned. Kentucky bluegrass, various species of bunch grass, wild roses, and *H. perforatum* were the predominant plants. A few scattered pine trees were present.

A total of 89 ant colonies were found, distributed fairly uniformly throughout the field. The nests were covered with the domes of detritus characteristic of the *Formica rufa* group of ants. The domes were six to 46 inches in diameter and one to 14 inches in height, with averages of 19.7 and 6.7 inches respectively. The detritus consisted mainly of stalks of *H. perforatum* but also contained grass and rose twigs. The surface of each dome was packed with pieces of bark, seeds, dirt, smaller twigs, and similar material so as to be relatively tight and weather-proof.

(1) Contribution No. 3481, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

Cole collected the type specimens of *F. subnitens* from a nest devoid of detritus (CREIGHTON, 1950). However, in recent studies COLE (1954) reported *F. subnitens* in nests similar to those described above but also reported this species nesting in shaded areas and under stones banked with detritus. The latter type of nest and nests in shaded areas were not found at Westbank.

The brood chamber was 10 to 12 inches in height and four to five inches in diameter in six average-sized nests examined. Smaller chambers were found below the brood chamber to a depth of three to five feet.

Foraging trails radiated from the nests. Some were well-defined paths worn into the ground whereas others were not discernible unless they were in use. The number and lengths of the trails, which varied greatly between nests, appeared to be related to the nature of the surrounding vegetation. A nest in an area of uniform vegetational cover had many obscure trails radiating in all directions. A nest in an area of mixed vegetation usually had one or more well-defined trails leading to the most productive food areas and a few obscure trails radiating to less productive food areas. The trails varied from three to 60 feet in length. The total area foraged by ants from each nest varied with the size of the colony but averaged about 2,500 square feet.

The ants in one nest of average size were anaesthetized and counted. The nest contained 20,118 worker ants. This did not necessarily represent a colony of average size because nest size is not an accurate measure of colony size: an old colony frequently had a large nest but very few ants whereas a young colony had many ants but a small nest. Moreover, a mature colony that vacated a nest did not construct a new nest of the same size as it vacated.

As field studies on *F. subnitens* were not started before May in either year, the brood development prior to this is not known. However, examinations made during May indicated that egg laying began during the latter part of April. By the end of May all larvae which developed from these eggs had pupated. Adults emerged about the middle of June. All adults emerging from this brood were sexuals. The peak of male emergence occurred one week earlier than that of females.

Oviposition was continuous from mid May to August. All adults that developed from these eggs were workers. Workers began emerging about the end of June.

Flights of sexuals occurred shortly after emergence, the ants flying from the nest singly. Flights occurred only between 8 and 10 a.m. and appeared to be induced by certain conditions of temperature and sunlight. Few sexuals took flight on cloudy days, even if temperatures were apparently favourable.

Sexuals were not observed mating. However, a few sexuals of *F. integroides* Emery, which has similar flights approximately three weeks earlier, mated on the nests before flight, suggesting that mating occurs mainly within the nest. *F. subnitens* possibly behaves similarly as this

type of flight disperses the sexuals and greatly reduces the chances of their mating after they have left the nest.

Formation of new colonies was not observed. The large concentration of nests in a relatively small area, as at Westbank, suggests that new colonies are founded by migrations from established ones.

Laboratory studies showed that this species does not require a winter rest period and if given the proper conditions remains active and reproduces throughout the winter. Therefore, the times required for brood development and the dates of sexual flight and worker emergence may differ with locality.

Field studies indicated that this species is active at soil surface temperatures between 51° F. and approximately 125° F. Consequently the period of yearly activity probably varies with locality and weather conditions. At Westbank the period of activity was from April to October.

Activity in the field appeared to be directly associated with temperature, but when the ants were reared at a constant temperature of 75° F. activity was observed to be positively correlated with light.

The food of *F. subnitens* consisted chiefly of other insects and of aphid secretions. In 1954, through systematic field collections of insects captured by the ants, it was determined that 39 per cent of the insect food consisted of Hymenoptera and 34 per cent of Coleoptera. *C. gemellata* was not found among the Coleoptera. In tests *F. subnitens* refused adults of *C. gemellata* as food. Of the Hymenoptera taken as food, 82 per cent were *F. subnitens* and other species of ants. Lepidopterous larvae formed 12 per cent of the insect food and the remaining 15 per cent consisted of Diptera, Homoptera, Hemiptera, and Orthoptera. The nature of the insects taken as food appeared to depend largely on their availability to the ants. Hence ground beetles, other ants, and lepidopterous larvae formed the largest portion of the insect food. With few exceptions, insect food taken by the ants was captured alive, and a majority of their prey were still alive when taken into the nest.

The exact quantity of aphid secretions taken by the ants was not calculated. However, though very little was taken in spring it was estimated that by midsummer over 50 per cent of the food consisted of these secretion. The ants appeared to be relatively indiscriminate in their choice of aphids and those most abundant on the vegetation surrounding a nest formed the main source of this food.

Summary.

At Westbank, British Columbia, nests of *Formica subnitens* Creighton were covered with detritus domes and were found only in unshaded areas. The foraging area of a colony averaged approximately 2,500 square feet and had one or more ant trails. Reproduction of sexuals commenced in April and the adults emerged about mid June. Sexual flights occurred between 8 and 10 a.m. Worker castes were produced from June to August. Worker ants foraged between soil surface temperatures of 51° and 125° F.

from April to October. The ant lived largely on other insects and aphid secretions, the latter being taken in small quantities in the spring but making up over 50 per cent of the food by mid summer.

F. subnitens apparently did not prey on *Chrysolina gemellata* (Rossi), a chrysomelid imported in an attempt to control common St. John's-wort, *Hypericum perforatum* L.

Acknowledgments.

The author wishes to thank Mr. J. H. (McLeod) of the Belleville Laboratory for constructive suggestions throughout these studies. Mr. W. G. Wilson and Mr. P. D. Wakefield, Westbank, B. C., assisted in most of the field studies. Mr. C. D. F. Miller, Entomology Division, Ottawa, identified *Formica subnitens* Creighton.

Résumé.

En Colombie Britannique, à Westbank, *Formica subnitens* sont couverts de dômes de détritits et se trouvent seulement dans les zones sans ombre. La surface de récolte d'une colonie s'étend à peu près sur 230 m et présente une ou plusieurs pistes de fourmis. La production des sexués commence en avril et les adultes quittent la fourmilière au milieu de juin. Les vols sexuels se produisent le matin, entre 8 et 10 heures. Les ouvrières sont produites de juin à août. Elles récoltent d'avril à octobre, lorsque la température au niveau du sol est comprise entre 10 et 50° C. Les fourmis vivent beaucoup aux dépens d'autres Insectes et des sécrétions d'Aphides ; celles-ci sont prises en petite quantité au printemps ; mais ces quantités augmentent ensuite jusqu'à constituer 50 % de la nourriture au milieu de l'été.

F. subnitens ne se nourrit apparemment pas de *Chrysolina gemellata*, Chrysomélid importé pour détruire *Hypericum perforatum*.

LITERATURE CITED.

1954. COLE (A. C.). — Studies of New Mexico ants XI (*Jour. Tennessee Acad. Sci.*, 29 [2], 163-167).
1950. CREIGHTON (W. S.). — The ants of North America (*Bull. Mus. Comp. Zool.*, 104).
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THE GROWTH AND DEVELOPMENT OF COLONIES OF THE ANT MYRMICA

by

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INTRODUCTION

Sufficient work has now been done on the sociology and ecology of this genus of ants in particular on the species *M. rubra* L. and *M. ruginodis* Nyl. (previously *M. laevinodis* Nyl. and *M. rubra* L. respectively, YARROW, 1955), to make a synthesis of those aspects relevant to colony growth and development worthwhile. Whilst there is no doubt that extensive factors such as food supply limit the growth of many colonies this aspect is not emphasised here: it has already been considered at elsewhere (BRIAN and BRIAN, 1951, BRIAN, 1956 b). Here it is assumed that when food is abundant and physical conditions ideal, colonies are limited by intrinsic factors (as happens in all other known organisms) and an attempt is made to discover what these may be and how they act. Theoretically, there appears to be a profound distinction between mortal colonies founded by one or more queens which allow no subsequent increase or even replacement, and potentially immortal ones that take in more queens and divide even though both may be found as subspecies of a single species. This study is confined to mortal colonies and reference to *M. ruginodis* may therefore always be taken to imply the subspecies *macrogyna* (BRIAN and BRIAN, 1949).

STAGES IN DEVELOPMENT

The brood processes from the start of a colony by a single queen to the stage when workers are present, have been described for *M. rubra* L. (BRIAN, 1951). Eggs are not normally laid in the autumn of the nuptial year, but they may be occasionally, although it is doubtful if they survive the winter. The following spring, eggs are laid that may give rise to workers; if they do not the colony may still survive for more eggs are laid in late summer, which give rise to hibernating 3rd instar larvae (some of the first batch may, too) and these yield workers early in the next summer. Thus, a queen may successfully start a colony, even though she does not have worker assistance until she is two years old. It is possible, though unlikely, that she can hold out longer. This stage may be referred to as the pre-worker stage.

Further stages can be defined after considering data (given in BRIAN and BRIAN, 1951, fig. 1) which shows that colonies of *ruginodis* collected in exposed (as opposed to shaded) areas give a curvilinear regression of average worker head-width on worker number. In the earlier paper, a simple exponential curve was fitted by ordinary regression methods; here a modified exponential curve has been fitted by eye, as this is more appropriate when larger colonies are involved as they will be shortly. Worker size (fig. 1) increases with colony size considerably in colonies of less than 300 individuals and then changes only slightly in larger colonies. When similar information derived from 12 colonies collected in winter (and descri-

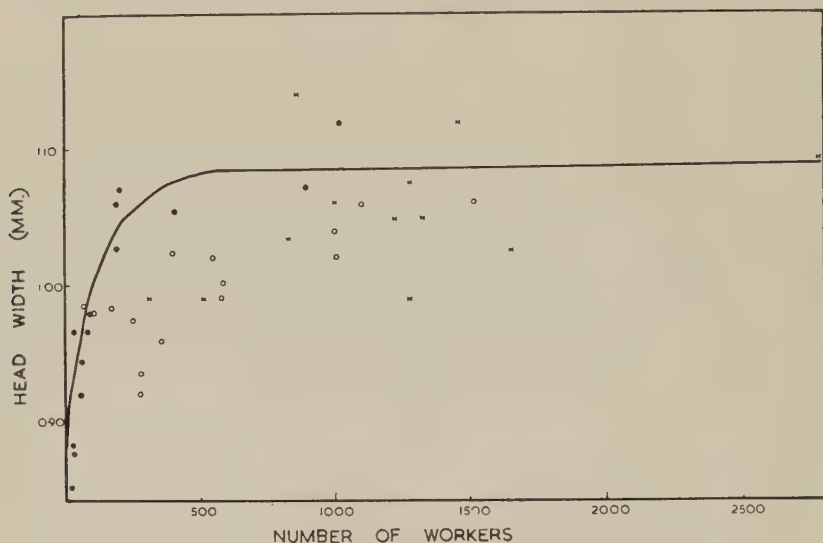


Fig. 1. — Mean head width in millimetres (y) plotted against colony size as numbers of workers (w). Black circles: nests from fully exposed situations fitted by the curve $y = 1.085 - 0.1835(0.678)w$; white circles: nests from shaded situations, no curve fitted (both sets of data from Brian and Brian 1951); crosses: nests collected from various situations in winter and analysed in Brian (1950).

bed in BRIAN 1950 table 3 and 4) is added to this it is found that, even colonies with as many as 2855 individuals, have workers with much the same average head-width as those of 300 (fig. 1). (This data on head width was not published in the first paper.) In terms of colony size the stage of increasing worker size accounts for about one tenth of the potential size; in terms of time, if growth is exponential, it may assume greater relative magnitude (see later). It will be referred to as the juvenile stage.

Brood has also been collected in early summer when it is mostly in the pupal stage and therefore easily separated into sex and caste types (BRIAN and BRIAN, 1951). Gyne pupae were present in all colonies with 854 brood units or more and in none with less (1). The next smallest had

(1) « Gyne » is used in the sense of pro-queen.

755 units and one may therefore conveniently take half way between, or 800 units, as an estimate of the minimum number for queen production. To convert this into an equivalent number of workers it is necessary first to estimate the number of winter larvae which it represents, and this can be done by using information on survival (given by BRIAN 1951) which states that 26 winter larvae gave 19 pupae in one year, and 48 gave 39 in the next. This gives a mean survival of 78 % and enables an estimate of about 1,000 winter larvae to be made. The worker equivalent can then be calculated from the regression of winter worker number on larval number (given in BRIAN, 1950, table 3) and a value of about 900 is obtained as the minimum size colony capable of yielding queens.

Male pupae were present in colonies with 553 brood units and over in exposed places but no nests between this and 13 units were sampled except from shaded areas which showed that males were produced in a colony with 336 units. Clearly, any estimate based on these figures must be very tentative, but a figure of 300 workers seems reasonable as a first approximation and it has the advantage of coinciding with that taken as giving maximal sized workers.

Thus, as a provisional classification of developmental stages, one may advance the following:

- (a) the pre-worker stage;
- (b) the juvenile stage, up to about 300 workers, of increase in worker size without the production of sexuals;
- (c) the adolescent stage, up to about 900 workers, when males but not gynes are formed;
- (d) the mature stage, when both male and female sexes are produced.

It is convenient to mention here that environmental conditions modify maturation appreciably; thus in shady habitats the average head-width of the workers is significantly less than in sunny ones, and such nests do not produce queens (BRIAN and BRIAN, 1951, BRIAN, 1956b).

THE JUVENILE STAGE

The increase in average size of worker which is the main feature in this phase of colony development, is a gradual process as the frequency distributions of table I show. Since it has been shown (BRIAN and BRIAN, 1951, table 8) that small workers are derived from small hibernating larvae, it is very likely *a priori* that the winter larvae of these juvenile colonies are small. Unfortunately, no really small colonies were obtained in the winter sample that was analysed (BRIAN, 1950), but to replace this deficiency seven small colonies were collected in early spring and the largest larva weighed and its maturity recorded in terms of the position of its brain (table 2) which moves slowly from head to thorax (see BRIAN, 1954). Since these colonies were collected in early spring when a little postwinter growth had occurred, the brain had in some cases moved out beyond the

TABLE I
HEAD WIDTH FREQUENCIES IN COLONIES OF VARIOUS SIZES.

HEAD WIDTH (1).	COLONY ARRAY:															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
26		1														
27		2														
28	1	3	3	6			3									
29	2	2	4	6	1		4	2		2						
30	2	1	2	2	3	1	6	5	4	2						
31			1	1	7	2	6	6	14	3	1		6			
32			1	1	7	7	3	5	13	4	7	4	8	1		
33					3	5	2	6	7	8	15	2	6	5	3	
34					3	6	1		3	5	8	10	4	12	9	2
35					1	3			1	1	15	5	1	17	14	5
36						1					4	8		12	15	14
37												12		3	8	14
38												8			1	12
39												1				3
Mean....	29.2	28.0	29.0	28.9	31.8	33.0	30.5	31.3	31.9	32.3	33.8	35.5	32.8	34.9	35.4	36.6
Total..	5	9	14	17	26	48	50	61	70	81	174	188	205	400	900	1,010

(1) In micrometer divisions : 1 division = 0.0303 mm.

normal winter range (0.0-0.6) so that although some were large (over 1.5 mg was the definition used in BRIAN, 1954) they were also mature and their actual stature was therefore quite moderate. Four of the largest larvae from each of the 7 colonies were cultured under ideal conditions, with fully prepared vernal workers from colonies that had produced sexuals, it being argued that this should give the larvae a chance to form queens if they had the potentiality; but in all 28 cases workers were formed.

TABLE II

THE WEIGHT AND MATURITY OF THE LARGEST LARVÆ IN SEVEN SMALL COLONIES IN SPRING,
AND THE RESULT OF IDEAL CULTURE.

NO. OF COLONY.	WEIGHT OF LARVÆ (mg).	BRAIN POSITION.	PROGENY.
1	1.1	0.7	worker
2	1.1	0.8	worker
3	1.7	0.6	worker
4	1.2	0.3	worker
5	2.4	0.9	worker
6	1.7	0.6	worker
7	1.6	0.9	worker

Thus the juvenile stage is evidently one in which small winter larvae yield small workers and reciprocally, small workers produce small larvae, and in which a gradual increase in the size of both takes place. The question then arises as to why such colonies are unable to produce large larvae. The most general answer is that they lack the food collection

power of the larger ones; they begin as solitary queens with no collecting power and only build up a worker force gradually. However, even if little food can be obtained, worker production could theoretically be so restrained that full-sized ones were immediately produced. The fact that they are not might be taken to imply a practical difficulty—and plenty can be conceived, perhaps the most obvious being the uncertainty of survival in the long course of development from egg to adult, which means that to reduce the chances of producing no workers at all an average number well above zero should be “aimed at”. Yet it is more than likely that the deployment of the small colony as minute units gives a better chance of success through the enhanced searching power conferred—even though this is at the expense of a reduction in size of prey and distance travelled. It is likely in fact that in ants that have adapted themselves to this style of colony foundation there is a selection favouring not only queens with large reserves, but also queens that lay small eggs (see GOETSCH 1939) or have other methods of suppressing size in their progeny. One of these has recently been described in *Myrmica scabrinodis* (BRIAN, 1956 a); it can operate, in spite of high worker/larva ratios and abundant food, on post-hibernation third instar larvae. The mechanism is unknown at the moment, but it certainly does not depend on distracting the attention of the workers by providing new brood from eggs laid, or by a high attractiveness on the part of the queen herself—for the larvae grow more quickly even though they pupate early and give small adults (which are all workers rather than mixtures of gynes and workers). The importance of the process may well lie more with caste control than growth control but its influence cannot be excluded in the latter case.

Hence the first workers are small, partly because they are produced by a system which allows for much wastage from the limited reserves of the queen, and partly because of some influence she exerts on their growth/development physiology (the first eggs are not detectably smaller than later ones). These workers feed the queen and no doubt she is soon entirely dependent on them and the food they import. Her egg production would be expected to be correspondingly small, even though she feeds herself on the carcasses of prepared prey rather than by receiving juices from the workers. Whereas there is plenty of evidence that solitary queens or *Myrmica* (and other genera) produce fewer eggs than they are later able to (BRIAN, 1951) actual experiments on the effect of worker number on output are hindered by the difficulty of distinguishing her eggs from those laid by workers. One can only be certain that the eggs counted are derived entirely from the queen, if observations are confined to short periods (2 weeks at 25° C, 3 weeks at 20° C) at the start of incubation when workers do not lay even when there are no larvae (BRIAN, 1953 a). In the first experiment a queen was set with either 6 workers and equal larvae or 130 workers and equal larvae and each treatment was replicated 5 times. The eggs that had accumulated after 3 weeks at 20° C ranged from 0 to 4 in the small groups and from 13 to 24 in the large groups, a conclusive

result. A second experiment provided for a range in worker number instead of two replicated extremes; one queen was set with either 6, 12, 25, 50, 100 or 200 workers and equal larvae, and after 3 weeks at 20° C there were respectively 42, 38, 44, 44, 70 and 85 eggs. This series regresses significantly ($P < 0.01$) on worker number with the equation:

$$e = 37.5 + 0.249 w \quad (e = \text{eggs, } w = \text{workers}).$$

Thus there is support for the likely *a priori* conclusion that the queen's egg production responds even if crudely, to the worker-population size. But this need imply nothing about whether they are more or less than the workers can manage; presumably it is more efficient if they are slightly in excess, so that at all stages in growth, the worker population is fully occupied and the cost is a little egg wastage (not a major loss as they are reabsorbed into the system). With a surplus of eggs the overloading of the workers and consequent maintainance of small size is not necessarily certain, for cases of adjustment of brood number to worker number occur (BRIAN, 1953 *b*). But were this to happen—and it might not, for it is quite likely that the queen increases conservation as part of her general catalytic action on brood rearing—the small size, and hence poor performance, of the workers to which the brood number was adjusted would surely ensure that only small additional ones were reared.

Into this system in which increase in worker size is restrained by the queen in various ways, and must anyway be slowed by the poor initial stature and feeble capabilities of the workers, there comes an increased power of food capture and preparation and it is very interesting to note that this food increment is not all absorbed by the queen, but reaches all the growing sections of the community, affecting the larvae and causing a slight increase above the size attained by their predecessors. This accounts for the gradual shift of size frequency which occurs.

ADOLESCENCE

By this stage the colony is evidently able to produce larvae big enough to become large workers but not big enough to become gynes. Males are however produced and derived parthenogenetically, one must suppose, from unfertilised queen-laid eggs or from worker-laid eggs. Such eggs may be laid in the juvenile stage and fail to survive its austerity, for in *Myrmica* as in many other ants male brood is less viable than female. On the other hand haploid egg production may only start after some change has taken place in the colony internal milieu—such as the aging of the queen, or the increase in size of the workers, or simply improved trophic condition which one assumes must exist, for there seems little doubt that the accumulation of worker-laid eggs is a sign of nutritional opulence (BRIAN, 1953 *a*).

On the whole, the bigger the colony the more males are produced, and

using the data given previously (BRIAN and BRIAN, 1951, tables 1 and 2) it can be shown that male number regresses positively ($P: 0.01-0.05$) on total brood with the equations:

$$y = 0.242 x - 40.0 \quad (y = \text{male number, } x = \text{total brood number}).$$

But there is much variability: perhaps due to a cyclic production in any one colony, males one year precluding males the next; or due to variation in food supply, for this affects the production and viability of worker-laid eggs (BRIAN, 1953 *a*).

MATURITY

Our knowledge of the mature state can be improved by reconsideration of the 12 winter colonies previously analysed (BRIAN, 1950, tables 3 and 4). Of these 8 had over 900 workers and were certainly mature, 2 with 835 and 850 workers might have been, and 2 with 577 and 305 were adolescent, according to our earlier definition. In these colonies there is no evidence of a continuation of the development shown by juveniles, for the average weight of larvae does not regress significantly on colony size ($r = 0.351$, $P > 0.1$). On the contrary, the dominant effects on larval size in winter appear to come from the ratio workers/larvae and the average size of workers. In the earlier paper the relation:

$$l = 0.308 R w \quad (l = \text{av. weight of larvae, } R = \text{ratio workers/larvae, } w = \text{av. weight of workers})$$

was derived. It may be added here that partial correlations support this as would be expected:

NORMAL.	PARTIAL.
$Rl + 0.637$	$Rl.w + 0.750 \quad (P < 0.01)$
$Rw - 0.041$	$lw.R + 0.659 \quad (P: 0.01-0.05)$
$Iw + 0.482$	

Both the normal correlations, only the larger one of which is significant, are increased by fixing the third variable. The situation may be depicted as a path diagram:

$$R \longrightarrow l \longleftrightarrow w.$$

What then affects these two factors: average worker size and worker/larva ratio? The former does not regress significantly on colony size (M) in this set of data for no really small colonies are present ($r_{wM} = 0.238$, $P > 0.1$). When these colonies are plotted (fig. 1) with the other data on headwidth in relation to colony size (the average headwidth was measured but not recorded in 1950) the majority lie between the regression lines for fully exposed and shaded colonies and it appears in fact that much of the variation in worker size (headwidth is proportional to weight) may be due to environmental variation (this influence is recorded in detail in

BRIAN and BRIAN, 1951 and BRIAN, 1956 b). Large workers, are of course, mainly derived from large winter larvae (BRIAN and BRIAN, 1951, table 8) and the existence of a nest in a good place should perpetuate this essentially reciprocal process. The worker/larva ratio does not regress on colony size either ($r = 0.221$, $P > 0.1$) and one can only suppose that these variations arise from failures to adjust the number of brood units produced to the number of nurses available as occurred in the experimental cultures discussed by BRIAN (1953 b). Whatever this failure may be due to, it bears no relation whatsoever to colony size, it could be chance, that is the result of many interacting factors, or it might be due to a breakdown in queen control: in higher ants, there is evidence that brood reduction through cannibalism which follows the loss or removal of the queens is associated with the production of sexuals (see BRIAN, 1956 a, 1957).

This then necessitates a modification of the views stated earlier (BRIAN and BRIAN, 1951), when it was suggested that sexuals might not be produced until the worker-force had outstripped the queen's egg production and a permanent and systematic rise in worker/larva ratio had occurred. But this idea need not be entirely rejected as the following considerations show. In the paper in which winter analyses were made, a curvilinear regression was fitted to the data on number of workers and number of larvae; it was better than a straight line as it reduced the error variance and went nearer the origin, as expected in theory. However, if the queen's egg output does limit colony growth, it might be thought that two straight lines would be theoretically more appropriate, one rising from the origin (larvae proportional to workers) and one lying horizontally (larvae fixed by the queen's egg production). Of the winter colonies, only one, of 2855 workers, is very large, and when it is omitted a very good linear regression relates the other eleven. Letting N = the number of larvae, and M = the number of workers, as previously, one may obtain the equation:

$$N = 1.23 M - 8 \quad (\text{S.E. of regression coefficient} = 0.229).$$

The error variance is only 85 % of that of the parabola fitted to all 12 colonies, and this line could easily arise in sampling from a population showing strict proportionality ($P > 0.9$). The largest colony with 2855 workers deviates widely from it on the side with fewer larvae than expected, and the best estimate of the second queen-output limited stage may be obtained by drawing a horizontal line at this level. This two-line method gives nearly as good a fit to the number data as the single line gave to the weight data (BRIAN, 1950): the coefficients of variation are 22.62 % and 20.77 % respectively. Not only does the largest colony with fewer larvae than expected lie close to the weight regression line (have large larvae) but in general those with more larvae than expected have them smaller than average or *vice versa*, a state which, of course, gives rise to the proportionality between average larval size and the ratio workers/larvae.

In this section of the paper it has been considered sufficient to argue that queens are produced when the ratio workers/larvae is high, because this has been shown to be associated with large winter larvae which in turn have been shown experimentally to be gyne-potential. Additional experimental evidence can be produced. Thus it has been shown (BRIAN, 1953 *b*, table 4) that higher ratios after winter give better yields of gynes. It has also been shown that large hibernating larvae are produced by the action of vernal workers provided the temperature is not too high (BRIAN, 1955) and this situation will normally arise in natural colonies if the overwintered larvae are quickly transformed into prepupae, a situation which results when the ratio workers/larvae is high. This same situation is likely to favour the generation and survival of worker-laid eggs for the larva-less period of the colony (BRIAN, 1951) will be prolonged, and although many of these eggs are likely to go to the female larvae, many may survive and so account for the frequency with which males and gynes are produced simultaneously in any particular colony.

A GROWTH MODEL

In this section a mathematical model of the growth of a colony of *Myrmica* is constructed and examined. Most of the facts are to be found in the two earlier papers already mentioned (BRIAN, 1950, 1951). In the later paper it was shown [that each summer two broods of workers are produced and some rather scanty data was given about their survival (in table 6 of that paper). Workers derived from hibernated larvae remain in the colony for 3 successive brood-rearing: one rapid (no larval dormancy), one retarded (dormancy during winter) and another rapid. Workers derived from rapid brood also survive whilst 3 more broods are reared, possibly even 4, but for simplicity it has been assumed that they die half way through their last summer so that they, like their sisters from retarded brood, nurse three successive broods. Lastly, it has been assumed that workers die according to a physiological life table, that is, altogether at the limit of their life span, an approximation which is not too severe in a preliminary model.

A difficulty arises since it is required to know whether a freshly emerged batch of workers has any beneficial influence on the larvae that emerge concurrently (for an account of the seasonal brood pattern see BRIAN, 1951). It is known that callow workers are for some time (at 25° C. 1-2 weeks) dependent on the older ones for food and take no part in brood rearing, and since they haunt the vicinity of the brood, they may actually interfere with its progress in more than one way. Further, they cause the older workers to leave the brood and forage (WEIR unpublished) a change which will only be beneficial if they are able to nurse effectively. To avoid this

dilemma two models have been made one with immediate beneficial action and one with this delayed until the next brood.

Immediate beneficial action

If y is the number of workers produced in the n th brood then

$$y_n = a (y_{n-1} + y_{n-2} + y_{n-3})$$

where a is a constant, is the model to be examined. It is a geometric recurrence relation, and like simple geometric series, no matter how they start they soon reach a steady ratio between successive terms. The main virtue of this system as far as population growth is concerned, is evidently that whilst providing a powerful expansion impulse, it guards against excessive chance fluctuations by making each increment depend upon more than that immediately preceding. Its action in this case recalls the smoothing process that can be achieved with a 3-way moving average.

As a method of solving this type of finite difference equation, it is customary (1) to try

$$y_n = A \lambda_1^n + B \lambda_2^n + C \lambda_3^n.$$

Then after setting up equations along the same lines for $-ay_{n-1}$, $-ay_{n-2}$ and $-ay_{n-3}$ and adding it is found that the three constants $\lambda_1 \lambda_2 \lambda_3$ are the roots of the characteristic equation

$$\lambda^3 - a\lambda^2 - a\lambda - a = 0.$$

This is much more easily solved if a is known, it is the ratio y_n/M_n where M_n is the number of workers at the n th brood and it can therefore be calculated from the winter larva/worker ratio if an adjustment of the larval number for mortality in transition to workers is made. In the colony of *laevinodis*, 26 winter larvae gave 15 workers in 1945 and 48 gave 36 workers in 1946; pooling these one finds that 74 larvae gave 51 workers in the 2 years so that the larval numbers should be reduced by about 2/3 rds. Since the larva/worker ratio was 3/2 for 3 successive winters, the constant a may be taken as unity, which simplifies calculations very much. Of the three λ roots only one is real and has the value 1.83; A is the starting value y_0 and hence the equation of growth is

$$y_n = y_0 \cdot 1.83^n$$

Since $y_{n+1}/y_n = 1.83$ and $y_n = aM_n$ it follows that

$M_{n+1}/M_n = 1.83$ and the ratio of successive populations should be λ . These are not easy to gauge exactly owing to their instability, and the two peak values in each year have therefore been taken. This gives the sequence 18, 26, 37, 55 and 53, with ratios between successive terms of

(1) I am indebted to Mr. J. G. SKELLAM for this advice.

1.4, 1.4, 1.5 and 1.0 averaging 1.33. Actual growth is therefore far less than that predicted by the model.

Delayed beneficial action.

The alternative method is the following:

$$y_n = a(y_{n-2} + y_{n-3})$$

and by a similar argument to that used above, it appears that a solution to the equation

$$\lambda^3 - a\lambda - a = 0$$

provides, since only one real root exists, the common ratio. When $a = 1$ as before, this gives

$$y_n = y_0 \cdot 1.33^n$$

so that the observed mean ratio is obtained.

Although the initial number of workers, that is the number that the queen manages to rear, has no effect on the rate of growth, it has a slight effect on the time at which a particular size is reached; thus the juvenile period takes 6 years if there are ten, and 8 years if there are three workers to start with; and maturity is reached after 8 years in the first case and 10 years in the second case.

In general it is likely that after a prolonged juvenile period of about 7 years, in which only 300 workers are added, the colony spurts into full maturity, adding about 600 individuals, in a further 2 years. After this the production and dissemination of sexuals and the limited reproductive power of the queen will break further growth; and there is more reason to suppose that the population will then fluctuate violently than that a steady level will be maintained. Only in species in which sexual production is small and controlled by the needs of the colony (as perhaps in *Eciton* and *Monomorium*) is there a possibility of population stability.

No precise data about the age of natural or even laboratory colonies exists and the nearest one can get is to consider the size in vegetation subseres of known age. In a felled woodland subseres 5 years old (described in BRIAN and BRIAN, 1951, table 13) 13 colonies were examined of which 12 were referred to as "small" or "medium" which meant, according to the definitions given, that all were juvenile. Such a growth rate is fully compatible with the model. In a 12 year old subseres of the same type, 9 large and 1 medium colony were recorded which means that 9 out of 10 were mature; and since the model allows 8 to 10 years for maturity, the two are again compatible. Thus the model appears to suit varied data brought together in a number of ways, and may be accepted as adequate for the present.

DISCUSSION

BODENHEIMER (1937) in reviewing some of the population problems of social insects collated evidence which showed that many colonies after a slow start grew rapidly (exponentially) to a limit. But this limit was not held and a decline or a series of fluctuations followed, due in many cases to the death of the queen and in others to an unknown cause which Bodenheimer delusively explains as "the limiting influence of organized or organism-like growth". Since then, BITANCOURT (1941) has fitted a logistic curve to data collected by AUTUORI on the number of craters above the nests of *Atta sexdens* (an index of population size), but in this case it is impossible to say what sort of a limit exists, if indeed one is reached at all, for just as maturity (the emergence of sexuals) is reached data cease. Although BITANCOURT considers that the queen's oviposition must increase to a maximum and then decline, he prefers to believe that the colony size is limited by the availability of forage (leaves for the fungus garden). Presumably, the material collected per individual decreases as the colony grows, so that a maximum total intake is reached, after which any further growth of the population results in failure to replace those dying and a return to the earlier level. This ignores the effect of sexual production and emission.

In *M. rubra* some evidence for a population maximum governed by a limited egg production exists; but this process seems to be less important than that due to fluctuations (perhaps chance ones) in the worker/larva ratio and sexual effusion. It should be recalled too, that other intrinsic factors may limit population growth; thus it has been shown that inefficiency increases with group size (see BRIAN, 1956 c). Although emphasis has been laid on such intrinsic controls here and it has been constantly assumed that environmental conditions are optimal, the part played by environment has not been neglected elsewhere (BRIAN and BRIAN, 1951, BRIAN, 1956 b), for low insolation (and its derivative conditions of food supply and temperature) has been shown to reduce both colony size and worker individual size (and hence the chances of gyne formation). It may well prove ultimately that all these and others operate under different circumstances: first a series of extrinsic restraints, and then a series of intrinsic ones.

Summary.

Colony growth and development is conveniently divided into stages: pre-worker, juvenile, adolescent and mature. The pre-worker stage is one in which small workers are produced by the queen from her body reserves. The juvenile stage is characterised by a gradual increase in the egg production of the queen, and in the size of the workers. No doubt this is partly due to an improvement in food capture but other factors also exist; of great importance is the influence that the queen exerts on the growth and development of individuals, an influence which is independent of population tension

The adolescent stage is transitional; in it males first appear. The mature stage is one of full-sized workers and male and female sexual production.

Gynes are produced when the ratio workers/larvae is high. This varies randomly in most colonies about a mean value, and the size of the dormant winter larvae is proportional to it; but the cause of the variation is unknown. A condition of gyne production is that the colony be in a favourable environment, for even in large colonies, poor insolation causes small individual size. Very large colonies, in which workers are greatly in excess of those needed to rear the brood are uncommon, and it is suggested that this may be due to the population instability which the production and dissemination of sexuals causes.

A model of geometric recurrence type is constructed which agrees reasonably well with the facts culled in various ways from different sources.

Résumé.

L'accroissement de la colonie et son développement se font en quatre stades : une période pré-ouvrière, suivie des stades de jeunesse, d'adolescence et de maturité. Le premier stade est celui où la reine engendre et nourrit des petites ouvrières à partir de ses propres réserves. Le stade de jeunesse est marqué par une augmentation progressive de la ponte de la reine et aussi de la taille des ouvrières. La cause en est, sans doute, dans l'amélioration du butin, mais pas exclusivement, et nous signalons notamment l'influence exercée par la reine sur la croissance et le développement des individus, cette influence étant indépendante de l'état de la population.

Le stade d'adolescence est un stade de transition ; c'est à cette époque que les mâles font leur première apparition.

Au stade de maturité des ouvrières ayant atteint une taille normale cohabitent avec des fourmis mâles et femelles.

Il apparaît des reines, lorsque le rapport ouvrières-larves est considérable. Dans la plupart des colonies, ce rapport varie au hasard autour d'une moyenne et il conditionne la grosseur des larves hivernantes ; nous ignorons la cause de cette variation.

Une colonie, même forte, comporte des sujets de petite taille si elle n'est pas soumise à un ensoleillement suffisant ; ceci prouve que les conditions extérieures sont essentielles dans la production des reines. Il est assez rare de trouver de fortes colonies où le nombre des ouvrières est de beaucoup supérieur au nombre d'individus nécessaire à l'élevage du couvain ; l'auteur pense que ceci peut-être dû à l'instabilité causée au sein de la colonie par la production et l'essaimage des sexués.

On peut établir une formule géométrique de renouvellement-type qui s'accorde assez bien avec les données collationnées de sources diverses.

Resumen.

Convenientemente, el desarrollo y crecimiento de la colonia puédese dividir en estados como ser : pre-trabajador, juvenil, adolescente y estado maduro. El estado pre-trabajador es aquel en que la reina produce de sus reservas, trabajadoras pequeñas.

El estado juvenil se caracteriza por el aumento paulatino en la producción de huevos por parte de la reina como también en el tamaño de las trabajadoras.

Sin duda, esto se debe en parte a la mejora en su aprovisionamiento pero existen también otros factores ; es de gran importancia la influencia ejercida por la reina sobre el crecimiento y desarrollo de individuales, influencia ésta independiente de la tensión de población.

El estado adolescente es transicional-en él aparecen por primera los machos. El estado maduro es uno de trabajadoras perfectas y de producción masculino y femenino.

Los genes se producen cuando la proporción de trabajadoras y larva es alta. Por casualidad esto varía en la mayoría de las colonias con un valor reducido y el tamaño de la larva en estado adormeciente en proporción, pero se desconoce por qué motivo ocurre la variación.

Una condición en la producción del gene es de encontrarse la colonia en un ambiente favorable puesto que aún en colonias grandes la insolación pobre produce tamaños pequeños.

Es extraño encontrar colonias grandes en las cuales las trabajadoras exceden aquellas que se requieren para la cría y sugiérese que puede ser que esto se debe a la inestabilidad de la población causada por la producción y deseminación sexual.

Prodúces pues, un ejemplo de recurrencia geométrica que conforma bastante bien con los datos escogidos en varias maneras y de distintas fuentes.

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SERIAL ORGANIZATION OF BROOD IN MYRMICA

by

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INTRODUCTION

The seasonal sequence of brood changes in colonies of *Myrmica rubra* L. in artificial nests with food supply but at natural temperatures has been described (BRIAN, 1951: at that time the species was called *M. laevinodis* Nyl.). Briefly, two brood cycles from egg to adult run concurrently in such a way that the eggs and first instar larvae (perhaps some second instar ones, too) of one accompany the prepupae and pupae of the other, and the second and third instar larvae of one are actively feeding whilst new workers are being produced from the other. This relationship is defined as being in opposite phase; it means that the whole colony passes through alternate embryogenic and trophic phases; the first when eggs, self feeding first instar larvae and pupae occur, and the second when larvae dependent for food on workers form the principal brood component. Each year 2 brood cycles are started (not one and a half as previously suggested) one early and one late in summer and whilst the first is completed (and will therefore be called the summer cycle) the second is interrupted by winter (and will therefore be called the winter cycle). The two cycles are not fully distinct for part of the first is held in the larval stage and joins the second. These facts may be summarized symbolically after considerable simplification; let E=eggs, L=larvae, P=prepupae and pupae, A=adults, M=embryogenic and T= trophic, then using lower case letters for small broods and upper case letters for large ones:

	SUMMER.	WINTER.	SUMMER.	WINTER.	SUMMER.
Brood cycles (winter).	PA ; eL		PA ; eL		PA ; eL
Brood cycles (summer).	EL $\frac{ll}{pa}$;		EL $\frac{ll}{pa}$;		EL $\frac{ll}{pa}$;
Colony cycle..	MT ; MT ;		MT ; MT ;		MT ; MT ;

An important virtue of this system is doubtless that the larval and worker populations are augmented simultaneously; by producing a new batch of eggs during the period of pupation of the preceding one new larvae are made available for the incremented worker population to deal with, so that the numbers established are as great as possible (see Brian, 1953 b). Similar principles have been demonstrated in *Bombus agrorum* (Brian and Brian 1948; Brian A.D., 1951) with the difference that the eggs are actually laid on the pupal cells and in numbers proportional to their size, and that several such cycles run concurrently without any apparent co-ordination.

Brood co-ordination was first described in species of *Eciton* by Schneirla (1944, 1949): in this genus the M and T cycles are associated with differences in colony behaviour :

colonies are sedentary in the M and nomadic in the T phase, and it is probably this which has forced the evolution (perhaps from a *Myrmica*-like prototype) of much sharper periodicity than is seen in *Myrmica*, a periodicity largely acquired through the ability of the queen to lay enormous numbers of eggs in a short time. In *Myrmica*, seasonal egg frequency is distinctly bimodal and arises usually from at least two causes: a periodism in queen oviposition and the fact that newly emerged larvae eat eggs and so destroy the egg mass from which they originate (for details see Brian, 1951). Thus even if the queen's oviposition continues all summer (as happens if delayed by a cool spring) the larvae are still generated in pulses. Another factor that splits the *Myrmica* brood into batches is the onset of larval diapause in the third instar late in summer. This divides the summer brood cycle into two distinct parts one of which fuses with the winter cycle as already explained. Its action although causing a reassortment of the brood series nevertheless creates a much more definite schism.

This paper is concerned with the processes that keep the two broods in opposite phase. Briefly, two types of mechanism are possible. In one, the parts and processes respond independently to some external governing factor and are so set by evolution that the required pattern develops; this may be called the "preset" type. For example, if the interval between successive periods of oogenesis were made equal to the time needed for eggs to change into pupae and if both responded to temperature in the same way, then the observed pattern could conceivably be produced. Or again, if queen oviposition was continuous and pulses of brood were generated by larval egg eating, it is conceivable that as the system reset itself for egg accumulation, the advanced larvae would start to prepupate: this necessitates a larval period roughly equal to both the incubation and the metamorphosis periods, but it is more automatic. In the other type of mechanism the parts and processes interact more or less frequently, so that one can only progress (at any rate beyond a certain stage) if the other does; this will be called the "regulative" type. For example, each period of oogenesis may be started by the queen receiving a signal from a previous brood batch as they become pupae—as must surely happen in *B. agrorum*; in *Eciton*, Schneirla believes that the pupation of the old brood deflects food to the queen and so initiates oogenesis.

DEPHASING EXPERIMENTS

To test for a regulative system the broods were set to start after winter in an abnormal time relationship. Either the queen or the hibernating larvae were detained at constant refrigeration temperature whilst the rest were incubated. In one experiment 20 workers, 20 larvae and one queen were used in each culture; either the queen or the larvae were delayed four weeks and each treatment was duplicated. When the larvae were delayed the queen began laying normally and by the end of the first week a few eggs were present in both replicates (Table I). Peaks of over 100 eggs were reached in week 3 in one and week 4 in the other culture, and it is clear that the queen can oviposit in the entire absence of larvae, which in view of the fact that she is able to found a colony in the first year by herself is not surprising. After the 4th week when the 20 larvae were added, new derived larvae were present: 15 in one and 28 in the other, but the added ones were immediately accepted and fed. They grew and metamorphosed without interruption giving a pupal and prepupal peak of 30 at week 7 in one case and a plateau in weeks 6-7 in the other. After minima in the 5th week, egg number again rose and attained double its

TABLE I

BROOD SEQUENCES IN COLONIES WITH EITHER QUEEN OR LARVÆ DELAYED BY 4 WEEKS.

TREATMENT AND REPLICATES.	BROOD TYPE.	WEEKS FROM START:										
		0	1	2	3	4	5	6	7	8	9	10
Larvæ late 1.	eggs larvæ pupæ (1)	0	5	54	81	103 35*	14 34	33 16 21	82 4 30	107	190	111 3
		*including 15 derived from eggs.										
Larvæ late 2.	eggs larvæ pupæ	0	6	96	104	79 48*	26 40 1	62 29 17	87 15 15	91 4 7	196	120 6
		*including 28 derived from eggs.										
Queen late 1.	eggs larvæ pupæ	20	20	11 8	10* 6 10	62* 10	91* 4	123	127	163 0	207 0	193 5
		*mainly or entirely worker-laid.										
Queen late 2.	eggs larvæ pupæ	20	20	14 5	28* 3 15	51* 18	65* 2	151	158	169 0	204 0	148 0
		*mainly or entirely worker-laid.										
(1) Pupæ include prepupæ in all cases.												

previous value in the 9th week, by which time there were no larvae. This fact combined with the presence of a number of large soft eggs, makes it likely that many were worker-laid (BRIAN, 1953 a).

When addition of the queen was delayed four weeks, the larvae were reared normally as is well known from previous experience. In both replicates all larvae were transformed by the 4th week and the number of eggs laid by workers was substantial (over 50). The queens, which were then added, were not at first accepted by the workers, even though they came from the same colony (a situation recalling that existing between laying workers and queens in *Apis*, *Bombus*, *Polistes* and others). They were actively menaced with jaws, but after 15 to 18 hours were left alone provided they kept away from the brood. They were accepted by degrees and in a week both had managed to reach and stand on the brood, and were evidently getting, food, for their gasters enlarged. (Such submissive

behaviour by queens is unusual: I have experimental evidence which shows that normally the queen selects the brood site in an artificial nest). As a result of this delay in acceptance oviposition was a week later than usual and the 6th week is probably the first to show queen-laid eggs, although these could not be distinguished with certainty from those laid by workers. Egg number rose to a peak of over 200 in the 9th week, and then declined whilst a few young larvae appeared in one replicate. This small production of derived larvae is noteworthy. It is unlikely to be due to a long incubation time for temperature was constant at 25°C in all cases, and in the larval treatments the normal time of 1-2 weeks for incubation was recorded. It is almost certain that the queens were laying as their gasters were noticeably enlarged as they only are in such circumstances. Nor is it likely to be due to low fertility for the other treatment cultures were normal in this respect; unless the subordinate status of the queen prevented by psychosomatic processes the fertilisation of the eggs—as occurs when certain parasitic Hymenoptera are given poor hosts (see Flanders 1946). It is also possible that the queen-laid eggs got mixed up with those laid by workers and for some reason, perhaps to do with the inability to distinguish one sort from the other, were mainly destroyed. Other evidence of this will be given later. Thus, this experiment shows that queen and larvae act independently and that there is not a continuous linkage between the processes associated with them; but it also shows that derangement can have disastrous effects on brood production as when reluctance to accept a queen interferes with the yield of larvae.

In the foregoing food was always abundant. This might be regarded as a defect in design for any trophic competition between queen and larvae could only be expected to show when food was short. An experiment was therefore set up in which, as before, either the queen or the larvae were delayed but two food levels were provided, one ample and one restricted (protein supplied only occasionally in small amounts). For further comparison a normal system (queen and larvae set simultaneously) and one lacking the queen altogether were set at the same two food levels. The previous experiment could also be criticised on the grounds that too great a difference in phase was produced, for larvae from eggs were already appearing when the wintered larvae were added. Therefore, in this experiment, the queen was added when larvae had reached the point of prepupation, after two weeks, and the larvae were added after the queen had had a week's start.

In the cultures with larvae added late the queen's egg-laying proceeded normally and egg frequency rose to a peak in the third week at both food levels, one or two weeks before the pupal peak (Table 2). Food shortage thus acted not to change the time but to change the size of the egg peak, and hence also the yield of new larvae; it evidently also hindered the transformation of larvae into pupae. An interesting unexplained feature is that the second egg maximum was later than the second pupal one. In general, there is nothing to indicate any causal linkage even under inani-

TABLE II

BROOD SEQUENCES IN COLONIES THAT ARE EITHER NORMAL OR LARVÆ DELAYED, OR WITH THE QUEEN DELAYED OR NO QUEEN AT ALL; EACH WITH AMPLE OR SHORT FOOD SUPPLY.

TREAT- MENT.	FOOD.	BROOD.	WEEKS:																
			0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Larvæ late.	ample	e	0	8	74	106	51	24	30	41	35	41	71	50	—	5	—	11	
		l			9	15	30	28	33	26	29	29	31	—	41	—	38		
	p	20	20	4	1		6	7	2	3	2	1							
	L P			13	15	7	1												
	short	e	0	18	20	25	20	4	0	3	23	27	38	40	—	7	—	1	
		l			2	11	16	18	15	11	7	7	11	—	11	—	7		
	p	20	20	14	4	2	1	1	2	2	1	1							
	L P			1	10	11	2												
Normal.	ample	e	0	4	78	141	62	21	6	13	22	36	45	48	—	22	—	0	
		l			4	38	54	60	63	63	59	57	53	—	53	—	53		
	p	20	20	4	3		2	2	0	0	0	2	—	2	—	0			
	L P			15	15	9	3												
	short	e	0	12	36	50	15	4	2	22	19	19	7	8	—	9	—	10	
		l			4	24	23	20	23	23	28	27	25	—	16	—	16		
	p									1	4	3							
	L P	20	19	16	12	7	5	4	2										
			2	5	5	6	3	1	2	2									
Queen late.	ample	e	0	0	0*	78	161	187	57	12	10	12	18	20	24	16	—	0	
		l						17	47	44	37	32	35	35	35	36	—	31	
	p								1	8	10	5	7	7	4	—	1		
	L P	20	20	11	2														
	short	e	0	0	0*	41	99	136	41	6	5	8	8	22	18	19	—	2	
		l						10	31	36	32	33	28	28	29	28	—	30	
	p											3	3	0	3	—	3		
	L P	20	20	12	5														
			6	10	10	5	4	1											
No queen.	ample	e			12	51	19	20	27	15	7	1							
		L	20	20	15	8	6	6	1										
	P			5	10	8	3	3	3										
	short	e					8	7	15	6	0	8							
L	20	20	16	14	10	5	2												
P				2	6	6	5	5	2	2									

* Queen added.

e = eggs; l = new larvæ; p = new prepupæ and pupæ; L = old larvæ; P = old prepupæ and pupæ; maximum italicised.

tion. In normal cultures the first egg and pupal maxima synchronise only if food is ample, for the retardation of larval growth caused by food shortage delays the first pupal peak; in fact food shortage acts to upset the phasing rather than to establish it. Again, lack of food does not affect the timing of the first egg peaks, only their size. The second egg peak in the culture short of food, even when allowance is made for its plateau character is rather surprisingly early and precedes the second pupal peak which however is very small. In the treatment pair in which the queen was added after two weeks, both first egg peaks were simultaneous and just two weeks later than usual, and the food-short one was smaller although both were very much bigger than in the other treatments. They occurred after the pupal peaks even though there was no hostility to the queens in this experiment. It is unfortunately not possible to say whether the eggs were laid by the queen or by the workers; in fact they were probably a mixture for the concurrence of pupae rather than larvae must have encouraged worker oviposition. As in the other pair the second egg peak is later than the second pupal one in the well-fed culture and very much the same, in spite of a certain vagueness, in the food-short culture; no explanation of this can be offered.

In all cases but one the second egg peak was smaller than the first. In the queen-late set this difference is at its greatest, less in the normal set and least in the larvae-late set (reversed in the food-short one). One is left with the impression that if conditions are favourable for the first oviposition period (as in the presence of pupae) the second suffers, but if conditions are unfavourable at first (as in the presence of larvae) the second gains. The queen may well have a limited seasonal capacity for egg production.

The cultures without queens add little information; they show the slow transformation of larvae into prepupae and the smaller and later egg frequency under conditions of food shortage. Unlike the cultures containing queens the egg production is closely correlated with the presence of pupae for eggs are either not laid or if laid are soon fed to larvae when these exist (BRIAN, 1953 a).

In general one concludes that if an alignment mechanism exists, it must be very weak; that queen-laid eggs unlike those laid by workers can accumulate in the presence of feeding larvae, and that food shortage does not cause alignment through increase in the competition between broods (indeed it may destroy it). Curiously enough, the second egg peak was after the second pupal peak when food was abundant, but when food was short, owing to the slowing down of the growth of derived larvae the difference was reduced or absent (although in this case little or no pupal peak occurred).

Recently, a weak link has been discovered in research with other aims. It has been shown that a queen of *M. scabrinodis* can hasten the growth and development of larvae in some unknown way (BRIAN, 1956). Should she be able to do this most strongly whilst laying then it would generate

a tendency to concurrent production of eggs and pupae. But the force is evidently not strong enough to do this if larvae are far from completely grown.

LARVAL TRANSFORMATION RATE

In the experiment just described, the normal treatment showed close synchronisation of the first egg and pupal peaks, in spite of the fact that the experiment was done at a constant temperature (25° C) whilst the *rubra* colony in which this was first seen, was kept at natural temperatures that trended slowly upwards with much erratic fluctuation. It is likely that this was a coincidence for at constant temperature when the egg peak is almost invariable the size and time of the pupal peak depends on the rate of transformation of larvae into pupae and this in turn depends on a number of factors which will be considered in this section. One of the most important of these is the maturity of the larvae: if they are small and immature they frequently, though not invariably, take longer than otherwise to reach the prepupal stage even if they give queens. Moreover, the competition between larvae for worker service has to be considered: larger larvae are favoured even to the total neglect of small ones (BRIAN, 1957). The

TABLE III

THE DECREASE IN LARVAL POPULATIONS OF VARIOUS SIZES WHEN CULTURED BY 20 WORKERS.

WEEK.	NUMBER OF LARVÆ.											
	10				20				30			
	replicates		mean rate		replicates		mean rate		replicates		mean rate	
	1	2	3		1	2	3		1	2	3	
0	10	10	10		20	20	20		30	30	30	
1	10	10	10	0	20	20	20	0	30	30	30	0
2	7	10	9	1	19	19	18	0	29	28	25	3
3	3	4	6	4	8	10	10	9	21	12	10	13
4	2	0	4	2	2	6	4	5	11	8	2	7
5	0		4	1	1	2	4	2	7	5	2	2
6			2		1	2	4		2	1	0	4
7			0		1	2	3		1	1		
Mean size of progeny (1)	40.86				40.32				39.21			
									38.55			

(1) Head widths in units of 0.03026 mm.
The highest rate of change is italicised.

rate of transformation has also been shown to increase with worker number (BRIAN, 1953 *b*) up to a limit set no doubt by the larval number itself. But it is not a simple function of worker number for the more larvae there are, the more transform in unit time when worker number is fixed. Worker power is, when larvae are few, employed to produce a few large prepupae, but when they are numerous it is employed to produce more smaller ones.

The results of an experiment with 20 workers and 10, 20, 30, or 40 larvae obtained randomly from a natural colony and cultured at 23° C constant are shown in table 3. The rate of change rises to a maximum in the third week in all (although nearly in the fourth week in the largest culture) and increases up to a limit of 13; beyond this the more larvae there

TABLE IV

THE DECREASE IN SMALL AND LARGE POPULATIONS OF SMALL OR LARGE LARVÆ WHEN CULTURED BY 20 WORKERS.

WEEKS	LARVÆ.							
	10				40			
	large		small		large		small	
	repli- cates	mean difference	repli- cates	mean difference	repli- cates	mean difference	repli- cates	mean difference
	1	2	1	2	1	2	1	2
0	10	10	10	10	40	40	40	40
1	10	10	0		40	40	38	39
2	4	2	7		38	39	35	38
3	0	0	3		17	12	30	29
4					5	4	19	22
5					3	0	16	15
6							14	13
7							11	8
8							6	5
9							4	2
10							4	1
11							2	0

The highest rate of change is italicised.

are the longer it takes to change them and the smaller they are. The effect of an experiment with both larval size and number varying together has been summarised in table 4: larger larvae are much more quickly changed into prepupae than smaller ones and the maximum rate of change is a week later with four times as many larvae (a feature hinted at in the previous experiment). Complete transformation of a large number of small larvae may take several weeks. Poor food supply has been considered as a retarding factor in this paper and earlier (BRIAN and BRIAN, 1951, table 8); it causes a reduced rate of change which takes longer since such

food as is available is not given to all larvae but concentrated on a few. Thus, in general, when larvae are superabundant in relation to nurses or to the external food supply work is concentrated on the largest so that transformation is more serial.

Within a certain range higher temperature accelerates the process of change but there is a threshold low temperature with quite a different effect (BRIAN and BRIAN, 1951). At 15° C growth is possible but prepupation is not, or not in most individual cases, so that larvae will grow up to the state immediately prior to prepupation and then stop. Under natural conditions this results in an accumulation of mature larvae which wait for the temperature to rise and then transform altogether. This is discussed and illustrated in a later section.

QUEEN OVIPOSITION

As it has been shown (BRIAN, 1953 *a* and here), that worker-laid egg accumulation is very sensitive to the larval population, or more strictly, to the worker/larvae ratio it is natural to enquire whether the same applies to eggs laid by the queen. To settle this is not easy since the two sorts of eggs are not certainly distinguishable by appearance, and it is possible that worker-laid ones may be mixed with queen-laid ones. But there are certain ways of circumventing this, none satisfactory to be sure, but for the time being useful nevertheless. One is to consider only the eggs that accumulate before workers are known to lay: this gives 2 weeks at 25° C or 3 at 20° C. Another way is to set controls without a queen and compare egg production, but this only leads to conclusions where differences are quite gross.

An experiment was set in which 20 workers cultured either 10 or 40 larvae with or without a queen, and each treatment was triplicated (table 5). The main brood sequences (details of replicates are omitted) show that even though the ratio workers/larvae covers the entire natural range (BRIAN, 1950) there is no major difference in egg-frequency (and certainly no statistically significant one) between the two treatments with queens. On the other hand there is a major difference in egg frequency between those without queens. Thus after two weeks there were averages of 46 eggs with 10 larvae and 37 with 40 larvae but the actual replicate values were 31, 45 and 63 in the first set and 38, 40, and 33 in the second set. One may note further that the bimodality of the egg distribution was more marked with 10 larvae. This is reminiscent of the difference between the years 1945 and 1946, in the *rubra* (= *laevinodis*) colony studied earlier (BRIAN, 1951) when there was good reason to suppose that the delay in the start, due to cold whether, made the relaxation phase small or non-existent, so that the queen laid more or less continuously all the season. In this experiment it might be suggested that the larger larval population withdrew much of the worker attention from the queen in the early stages, but

TABLE V

AVERAGE BROOD SEQUENCES IN CULTURES OF 20 WORKERS WITH 10 OR 40 LARVÆ WITH OR WITHOUT A QUEEN.

TREATMENT		BROOD STAGES.	WEEKS:												
QUEEN.	LARVÆ.		0	1	2	3	4	5	6	7	8	9	10	11	12
One.	10	e	0	21	46	51	37	26	13	17	13	27	29	28	14
		l (1,2)	0	0	0	4	10	8	9	1	0	1	2	3	4
		1+L(3)	10	10	7	3	3	8	13	19	20	18	18	19	19
		P	0	0	3	6	8	5	3	1	1	2	2	1	0
	40	e	0	19	37	38	46	41	28	26	27	30	19	7	2
		l (1,2)	0	0	0	6	12	6	11	4	5	7	6	6	4
		1+L(3)	40	40	31	20	13	13	15	19	22	23	25	27	27
		P	0	0	2	5	24	24	15	8	5	4	2	2	1
None.	10	e	0	0	0	19	78	91	49	23	discontinued				
		l (1,2)							5	3					
		1+L(3)	10	10	9	4	2	1	1	0					
		P	0	0	1	6	7	6	3	2					
	40	e	0	0	0	3	10	25	29	36					
		l (1,2)							1	1					
		1+L(3)	40	40	37	28	13	7	5	4					
		P	0	0	3	15	25	26	14	7					

e = eggs; l = new larvæ; L = old larvæ; P = prepupæ and pupæ;
 The figures in parenthesis in column 3 indicate the instar of the larvæ, whether new or old.

compensated later when the larvae had pupated, but the differences are not statistically significant. The later egg peak in the 10 larvae/1 queen cultures brings the first egg and pupal maxima closer together. Curiously little non-dormant brood was produced by either set of cultures and no second pupal peak exists; this shows the independence of oviposition and pupation in the second part of the annual cycle. Most of the new brood became dormant but the quantities produced: 17, 19 and 26 in the 10-larvae set and 25, 27 and 29 in the 30-larvae set, are not statistically different. The numbers of first and second instar larvae together were greater at all censuses in the 40-larvae/1 queen set than the other (except at week 5) on the average, but again this difference is not statistically significant. Even so, there are indications worth further study that the cultures with more winter larvae did better; the larvae may serve as a food reserve or just as a steadying influence on the workers.

The sets without queens dealt with their larvae at much the same rate as those with. This data may be subtracted from the total third instar

larvae in queenwith cultures when it gives an idea of the number of new ones present. Worker-laid eggs were much more abundant in the 10—than in the 40—larval set, and after rising quickly to a peak fell just as quickly as new male larvae emerged. Worker-laid eggs are unquestionably an index of larvae sparsity. Quite clearly there is here strong evidence that the queenwith cultures did not accumulate eggs laid by workers, perhaps because the queen eats them herself, or perhaps because she produces larvae that do so: there were 10 to 12 young larvae in the 1st and 3rd instars present at the time. Even so, the number of larvae seem small to control the enormous quantity of worker laid eggs that appear in the queenless cultures, and some other repressive mechanism may well be involved.

This experiment shows strikingly how little, if at all, the queen's egg production is influenced by even major variations in the winter larval population; in this it contrasts markedly with worker egg production. The queen and her egg-mass appear to be independent of the rest of the colony.

In a further experiment 20 workers and 1 queen were continuously saturated with winter larvae; they started with 40 and more were added as these metamorphosed. By contrast, another lot had only 10 larvae to which no more were added. The first treatment was replicated 8 times,

TABLE VI

EGG FREQUENCY IN LARVA-SATURATED AND LARVA-FEW CULTURES, EACH WITH ONE QUEEN.

TREATMENT.	REPLICATE.	WEEK:									
		0	1	2	3	4	5	6	7	8	9
40 larvæ at first; then others added to saturate.	1	0	10	47	80	60	63	101	53	44	45
	2	0	0	25	68	60	68	82	71	85	41
	3	0	10	25	30	40	37	48	59	63	51
	4	0	3	25	50	74	86	105	50	52	66
	5	0	15	109	115	47	130	159	123	109	31
	6	0	7	23	25	27	33	41	42	29	47
	7	0	11	48	61	44	48	58	65	48	45
	8	0	10	69	122	74	75	101	67	52	50
Mean.		0	8	46	69	53	68	87	66	60	47
10 larvæ at first; none added later.	1	0	20	56	35	19	37	61	36	4	6
	2	0	12	78	128	79	31	51	65	48	49
	3	0	19	32	60	57	43	35	38	41	35
Mean.		0	17	55	74	52	37	49	46	31	30
Maximum italicised.											

and the second 3 times. The egg frequency for 9 consecutive weeks has been given in table 6. There are no statistically significant differences at any census; during the first four weeks the average differences are very small, but in the second phase the differences are greater, although still not significant; there seems little room to doubt that the larval population has no influence (comparable in size with that of intrinsic variation), on the queen's egg production. Once again, there is a slight indication that poor early output is later compensated.

THE NATURAL SEASONAL CYCLE

Thus as no adequate regulative mechanism has been discovered, search must be made for a preset one. Of all the possible governing factors temperature is the most likely; and the natural seasonal processes will now be considered with this in mind.

SPRING

It has been shown that when a colony is suddenly brought from refrigeration condition (0-3° C) up to incubation temperature (20-25° C) both the queen and the larvae respond and whether or not the first egg and pupal maxima coincide depends mainly on the character of the larvae and on the larva/worker ratio and food supply. The queen is more or less independent of all but the last. However, in natural conditions, the rise in temperature is gradual and fluctuating, and in view of the earlier demonstration that the threshold of larval growth is below that of prepupation it seems *a priori* likely that each year a variable proportion of the larvae may have the opportunity to grow and await the rising temperature which releases prepupation and either releases oviposition, or if it has already started, stimulates it. With this in mind, the data collected from the colony of *rubra* (= *laevinodis*) at natural temperatures (1) that has already been published in part (BRIAN, 1951) may be further considered. In table 7 the times to the nearest week in each month (which is divided roughly into four parts) at which larval growth, egg accumulation and prepupation started and stopped and the average temperatures of the week in question have been given. It is quite apparent that whilst there is a good deal of variation in the time at which these three processes start each year, there is less in the temperature: each is evidently released when the temperature reaches a certain value, and these values as can be seen from the table, rise from 7-8° C for growth to 10° C for egg accumulation and to 13-14° C for prepupation. The simple fact that prepupation

(1) Taken under 4 inches of soil at 9.00 hrs each day. They can only be taken as an index of seasonal temperature for in nature colonies move up and down in the soil and seek their preferred temperature; and of course, 9.00 hrs is almost the coolest time of day.

TABLE VII

THE WEEK IN THE YEAR AND THE CURRENT MEAN TEMPERATURE AT 9.00 HRS AT WHICH THREE PROCESSES STARTED AND STOPPED IN A COLONY OF *Myrmica ruba* L.

PROCESS.	YEAR.	TIME OF START.	TEMPE- RATURE in °C.	TIME OF FINISH.	TEMPE- RATURE in °C.	DURA- TION (months).
Larval growth.	1944		—	October I	11	—
	1945	March IV	7	October II	11	6.5
	1946	April I	7.5	October II	10-12	6.3
	1947	April III	8	October II	12	5.8
Egg accumulation.	1944	April III	9	September II	14	4.8
	1945	April II	10	August II	15.5	4
	1946	April IV	10	September II	14	4.5
	1947	May IV	10.5	—	—	—
Metamorphosis.	1944	June I	14.5	September II	14	3.3
	1945	April III	13.5	August I	17	3.5
	1946	June II	13.5	August IV	14.5	2.5
	1947	June I	16.5*	—	—	—

* Previous week 13° C.
Each calendar month is divided into four parts indicated by Roman numerals.

starts at the same temperature each year, shows clearly that it is released by temperature, that is, that there are always some larvae ready to change. In 1945 there seemed to have been a smaller proportion ready than in 1946 when a great many accumulated in the largest size group (BRIAN, 1951, table 2).

Another point of interest is the variation in the interval between the various starting dates. To further illustrate the temperature-dependence of this, the main temperatures for the three seasons 1944-6 have been figured (fig. 1) with the times marked at which the three processes started. In 1944 and 1946 the interval between the first egg and the first prepupa (5-6 weeks) was evidently due to a cool May, for in 1945 when only a week separated them the second half of April was exceptionally warm. However, at the end of the month and early in May, very cold weather with snow supervened and stopped both processes for two weeks. The dip in production which this caused could be traced right through to September. The data brings out one more point: that although eggs can be laid and accumulate at a lower temperature than that which enables larvae to prepupate, their greatest rate of increase occurs later. The very small rise in egg number in 1946 was due to the cold May already mentioned when temperatures ranged about 10° C for 4 weeks after the start of oviposition.

Later, as the temperature reached 12-13°C in the early part of June, eggs accumulated quickly and larvae prepupated after a long delay.

Thus, the association of the first egg and pupal maxima appears to be due to the low threshold of larval growth which enables some if not most to reach a stage when they are ready to prepupate. This they do when the temperature rises sufficiently high, and if meanwhile egg accumu-

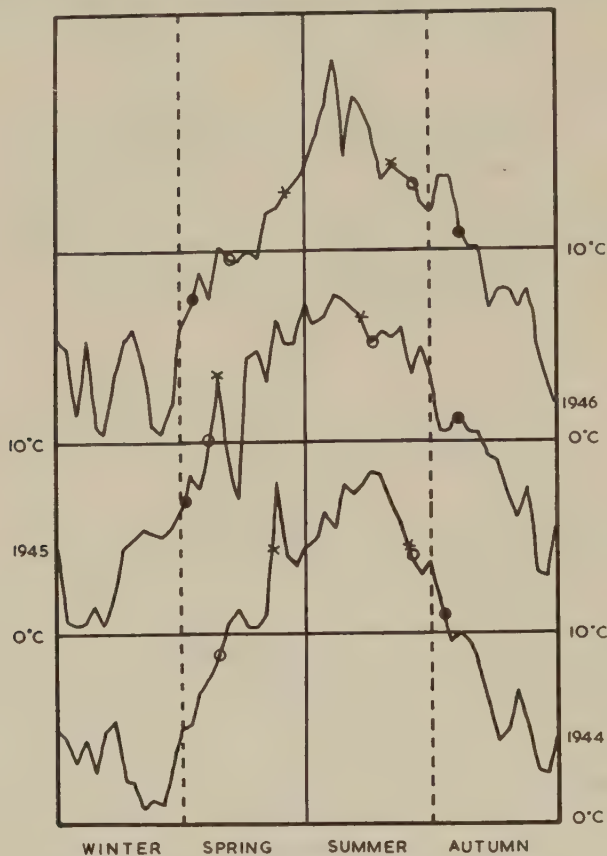


Fig. 1. - Temperatures at 4 inches below soil surface at 9.00 hrs averaged weekly for the 3 years 1944-1946. The dates at which the three important brood processes started and stopped are marked; black circles: larval growth; white circles: oviposition; crosses: prepupation. Ordinates: temperature in degrees centigrade; abscissa: time in weeks with winter and summer solstices and spring and autumn equinoxes marked.

lation has started, it also receives a stimulus from the same rise of temperature. The association of these two processes is thus externally imposed and depends upon the fact that winter prepares larvae, workers and queens for immediate response to warmth (BRIAN, 1955) and that the gradual spring rise sets off the different processes in a way which ensures that egg production starts before prepupation but that the major steps in both occur simultaneously. This "readiness" for spring, no doubt

also favours the action of the weak queen linkage mechanism. It is possible that worker oviposition may contribute something to the first egg peak (but not the second) if the larval population falls very low.

SUMMER

An important feature of co-ordination once the seasonal cycle has started is the isochronism of the incubation and metamorphosis periods over the natural temperature range. For brevity these will be symbolised i and p respectively. Thus the data given by BRIAN (1951) shows that i declines from 7 weeks in early summer to 5 weeks in high summer and p declines from 7 weeks (exceptionally 8) to 5 weeks in the same way. And so the seasonal pattern started in spring with broods in opposite phase and eggs slightly in advance of pupae continues in the summer with the synchronous appearance of new workers and second and third instar larvae (larvae hatch and pass through one instar before any workers emerge).

Of further importance is the fact that the duration of the larval stage reaches its minimum at this time of year (rapid brood) and like i and p has the value 5 weeks (BRIAN, 1951). The importance of this is considerable when the bimodality of egg frequency is due to the interaction of larval egg-eating with a continuous queen oviposition. Taking the simple case when she lays at a constant rate without interruption and assuming that each hatching larva eats one newly laid egg (different assumptions from those made in BRIAN, 1951, but equally probable and easier theoretically) then after a period of egg accumulation of time i larvae will begin to hatch. Since they destroy one egg in addition to that from which they emerge they will exactly neutralise the queen's production and the egg number will fall to zero whilst the larval number rises simultaneously to equal the prior egg peak at time $2i$. Next a new period of egg accumulation will start and repeat the first; and meanwhile the larvae will grow and begin to pupate, and if this is to proceed concurrently with the second egg increase, the period in the larval stage must be i which in fact it is. This system produces frequency oscillations with wave length $2i$ or 10 weeks; in practice they were 9 and 8 weeks for eggs and 10 and 8 weeks for pupae and prepupae (BRIAN, 1951, years 1945, and 1946 respectively). So, the correspondence between theory and practice is as good as can be expected with a crude theory and ill-defined natural peaks.

AUTUMN

Probably all the larvae from the second batch of eggs become dormant and hibernate. As a result of this, and because the queen stops laying too, the second colony cycle is abridged and it is necessary to look for terminating factors. The data of the *rubra* colony indicate that the end of the

period during which larvae are transformed into pupae is not always set by low temperature for in 1945 it occurred early in August at a temperature of 17° C whereas in 1944 and in 1946 it occurred later at a temperature much nearer the spring release value. In 1944 it was noted that metamorphosis slowed down until as long as 6 weeks were spent in the pupal stage, and the last two individuals to reach it were destroyed whilst still white after one and three weeks respectively. Prepupation in 1945 began much earlier than in the other two years, and the fact that it ended earlier, at the height of the summer, even though it lasted for 3.5 months, longer than in the other two years, suggest the existence of some internal limitation. In the other two years the late start evidently prevented completion and the total duration was less than maximal.

It has been shown (BRIAN, 1955, WEIR unpub.) that dormancy in larvae is due to the action of workers, and that these change as the season advance from actively laying types into non-laying diapause types with growing fat bodies. The exact way in which they act on larvae is not known but it appears to involve a change in the food administered, for non-dormant brood seems to get more sugar and egg and less crude flesh protein than dormant. Whatever the mechanism, it is evident that since the change in workers can be brought about in the laboratory in winter by simply making them work it is likely to mean that in nature an early start brings about an early conclusion to the metamorphosis season. The spring type of worker physiology can be restored by resting at low temperature as normally happens over winter.

The end of egg accumulation is in the week following the second peak, and it is quite likely that it represents the end of any major oviposition too. It is rather striking that it stops within a week or two of the end of prepupation even in 1945, but the hypothesis that a social linkage is effected through an action by workers on both the larvae and the queen, which brings about dormancy in both, is not supported by the experimental data given earlier in this paper. That data shows that the queen has an independent bi-periodic oviposition rhythm with a limited seasonal capacity for egg production. Evidently, the queen and the workers change simultaneously and independently as the season passes.

The close of the season is marked by larval growth alone; it is confined to the small larvae as can be seen from frequency distributions for the *rubra* colony (BRIAN, 1951) and as has been confirmed experimentally (BRIAN, 1955). As a consequence, a considerable larval population all in the third instar is built up. It is interesting that the autumn temperature limit appears to be a few degrees higher than the spring one.

DISCUSSION

The evidence then, favours a preset serial organization co-ordinated each spring by the rise in temperature which initiates sequentially larval

growth, oviposition and prepupation. The early low temperature growth of larvae ensures that some at least are able to prepupate when the temperature rises high enough—otherwise the excessively heavy load of larvae that is carried during winter and the fact that the queen's oviposition is unrestrained, would result in the pupal peak coming too late. After spring coordination the two brood cycles run together as a result of isochronal incubation and metamorphosis periods which cause the young larvae to hatch a little before workers emerge and so enables them to reach their second and third instars—stages when their food demand from workers is at a maximum. These prepupate in due course but the question: why do eggs again increase in numbers? is not yet clearly answered. There are two possibilities: if the queen's ovulation is periodic as it often is, then the interval between successive periods must be equal to the time taken from egg to pupa, and be established so by natural selection; if it is not periodic (and the bimodality of egg frequency due therefore to larval egg-eating) the fact that the time spent in the larval stage by the rapid brood is equal to the incubation and metamorphosis periods ensures that prepupation will accompany the second egg accumulation. The season closes not by letting this second colony cycle go to completion but by a nearly synchronal although independent change in workers and queen which arises through some physiological change based on the season's activity; it causes a dormancy which is transmissible to larvae and so stops further prepupation. The hibernation of larvae is clearly an adaptation to a micro-thermal climate (see BRIAN, 1951) but it unquestionably upsets the rhythm of the preset cycle that operates in high summer. It upsets it apparently by causing larvae to accumulate so that the worker force may be fully and profitably occupied during the cool "fringes" of the season; and as a result of this, the next season's brood processes cannot all start simultaneously (as would be simplest if the efficiency of serial organisation were the only factor to be considered in adaptation) for if they do the egg peak comes relatively too early. To this situation must be added the action of the queen which promotes growth of larvae and early prepupation, an action which may (although this is unproven) be stronger when she is laying.

Spring brood coordination is of course common in non-social insect populations: in the Collembolan *Isotoma viridis* for example. In this species eggs laid over a wide range of time in autumn hatch simultaneously, a fact which is due to the ability of the organism to develop during winter combined with its inability to emerge from its shell until warm weather arrives. During the summer this close synchronisation is progressively lost.

An essential feature of the *Myrmica* cycle is the isochronism of metamorphosis and incubation (and in one set of circumstances of larval life too). It is interesting to note that this is not normal in hymenoptera, not even in other ants. Thus in *Oecophylla longinoda* at 25° C incubation lasts 9 and metamorphosis 18 days (LEDoux, 1950); in *Eciton hamatum* at

natural temperatures the corresponding figures are: less than 10 days and about 19 days (SCHNEIRLA, 1944); and in *Monomorium pharaonis* they are, at 27° C, 7.3 and 12.1 days (PEACOCK and BAXTER, 1950). In *Eciton* this inequality does not affect coordination which is, as already stated, of the regulative type: pupation of a batch of brood sets off oogenesis; and after a few days there is a brief and copious oviposition, which still leaves time before the workers emerge for larvae to hatch and grow to a size necessitating food collection.

Presumably the isochronism of these processes in *Myrmica* has evolved in virtue of the improved serial organization which it confers.

Summary.

In the ant *Myrmica rubra* L. (= *laevinodis* Nyl.) two brood cycles (from egg to adult) run concurrently, and are so phased that eggs and pupae occur together and larvae hatch when new workers are appearing. The mechanism of coordination is investigated. Dephasing experiments in which either the queen or the larvae are added late, although affecting performance adversely in the former case, do not bring to light any strong intrinsic alignment mechanism, even when food is short.

The factors affecting the shape and size of brood-type frequency distribution peaks are considered. The pupal peak is later if larvae are small and numerous, or if food is short; and in these conditions worker attention is concentrated on relatively few of the largest. Temperature, if above prepupation threshold, hastens the peak. The egg peak is not much affected by wide variation in the larval population, but is substantially smaller if food is short. There is evidence that the queen's total annual output is limited so that a bad start may be later compensated or *vice versa*.

Extrinsic co-ordinating influences are then considered, and it is found that the temperature relations of developmental processes may be adapted by natural selection so that the brood pattern is set in motion and controlled each year by the rise and fall in mean temperature. By spring, the whole colony is ready to respond to warmth, and larval growth, oviposition and prepupation start in that order. Once set in step in this way they so remain owing to the isochronism of incubation, metamorphosis and larval life. The season closes when as a result of independent parallel changes in queen and worker respectively, oviposition ceases and larval dormancy gives way to prepupation.

Résumé.

Chez la Fourmi *Myrmica rubra* L. (= *laevinodis* Nyl.), on remarque deux cycles de couvaison (depuis l'œuf jusqu'à l'insecte adulte) qui se déroulent simultanément et qui sont ordonnés de telle façon qu'il se trouve en même temps des œufs et des nymphes et que l'éclosion de larves correspond à l'apparition de nouvelles ouvrières.

Examen du système de coordination.

Les expériences introduisant des erreurs de phase par suite de l'introduction tardive de la reine ou des larves ont, dans le premier cas, relevé une influence défavorable à l'évolution normale; néanmoins, elles n'ont mis en lumière aucun mécanisme d'alignement essentiel, même lorsque l'alimentation est restreinte.

Étude des agents pouvant modifier la forme et l'ampleur des pointes de la distribution de fréquence de couvées-type. La pointe de la nymphose est retardée si les larves sont nombreuses ou s'il y a carence alimentaire. Dans ces conditions, les soins des ouvrières visent particulièrement un petit nombre de larves choisies parmi les plus

grosses. Si la température subit une hausse alors que la nymphose se prépare, elle active l'apparition de la ponte. De grandes variations de la population larvaire modifient peu la ponte de ponte, mais celle-ci est sensiblement réduite par une carence alimentaire.

On peut démontrer que le rythme de ponte de la reine varie au cours de l'année; de ce fait, un mauvais début peut être compensé par la suite et réciproquement.

Si l'on étudie ensuite la coordination des conditions externes, on trouve que les rapports existant entre les températures de développement sont susceptibles de s'adapter par sélection naturelle; en conséquence, la marche de la couvaison s'amorce et se règle ensuite chaque année sur les variations de la température moyenne.

Dès le printemps, la colonie entière est à même de réagir à la chaleur et, quoique des températures modérées n'empêchent ni la croissance des larves ni une légère ponte, la préparation à la nymphose et la ponte abondante ne se déclenchent qu'après une élévation sensible de température. Ainsi commencés, les deux cycles se développeront de pair, puisque l'embryogenèse et la métamorphose accusent toutes deux le même mouvement périodique. La saison se termine lorsque, par suite de modifications s'opérant en même temps mais indépendamment chez la reine et les ouvrières respectivement, la ponte cesse; l'engourdissement de la larve cède alors le pas à la préparation de la nymphose.

Resumen.

En la hormiga *Myrmica Rubra* L. (= *Laevinodis* Nyl.), concurren dos períodos de cría de huevos a adultos en cuyas fases los huevos y crisálides ocurren juntos y la larva sale al mismo tiempo que aparecen las nuevas trabajadoras.

Se investiga el mecanismo de coordinación. Experimentando con las fases es decir, agregando mas tarde ya sea la reina o la larva, aunque afecta adversamente el funcionamiento de la reina, no se produce ningún mecanismo esencial de alineación aun cuando es poco su alimento.

Se consideran los factores que afectan figura y tamaño de pico de distribución de frecuencia del tipo cría.

En las crisálides, el pico ocurre más tarde si la larva es pequeña y numerosa o si el alimento es escaso y en estas condiciones la atención de la trabajadora se concentra sobre relativamente pocas de las más grandes.

La temperatura si sobre comienzo de la crisálide, adelanta el pico de distribución. En el huvo el pico no se ve muy afectado por la variación en la población de la larva pero es considerablemente mas pequeña si escasea el alimento.

Es evidente que la producción total anual de la reina es escasa asi que un mal principio compensariase quizá, o vice versa.

Luego se consideran las influencias de coordinación ajenas y se encuentra que la relación de temperatura de procesos de desarrollo se pueden adaptar por medio de selección natural asi que se empieza el tipo de cría y se controla anualmente por el aumento y disminución de temperatura. Al llegar la primavera, toda la colonia esta lista para el calor y aun cuando puede crecer la larva y puédense poner algunos huevos a temperaturas medianas no es hasta que ocurre un aumento importante que empiezan el estado pre-crisálide y colocación de huevos cuantitativa. Una vez empezado esto permanecen juntos puesto que la formación del embrio y metamorfosis, toman el mismo periodo. La temporada se cierra cuando como resultado de cambios paralelos independientes en la reina y trabajadora respectivamente, cesa la colocación de huevos y adormecencia larval da lugar al estado pre-crisálide.

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THE PROCESS OF QUEEN SUPERSEDURE IN COLONIES OF HONEYBEES (*APIS MELLIFERA* LINN.)

by

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INTRODUCTION

Queen supersedure, the process by which a colony of honeybees replaces its queen without swarming, is a frequent occurrence. Usually the worker bees of the colony concerned start to rear only a small number of new queens, either from fertilised eggs in special cells (queen cell cups) or from young worker larvae whose cells the adult workers modify for this purpose (emergency queen cells). It seems to be generally believed that the eggs found in such queen cell cups have been placed therein by the old queen herself (e.g. SNELGROVE, 1946) but in the case of supersedure this belief appears to be based more on supposition than upon observation.

Only one of the resulting virgin queens is normally allowed to emerge and remain within the colony, the others being destroyed in their cells by the workers or, possibly, by the first virgin queen to emerge. It seems likely, however, that occasionally two virgin queens will emerge simultaneously, but if this happens only one remains within the colony. Whether the other is killed by the other virgin or by the workers, or whether she leaves the nest with a small swarm, is unknown. All being well, however, the surviving queen mates in the field and returns to her parent colony to replace her mother, the old queen, as the colony's reproductive unit. No new colony is formed—with the possible exception mentioned above—and in this important respect the process of queen supersedure differs radically from that of swarming by which colony reproduction is achieved, and in which one or more new queens are also reared and the old queen leaves the parent nest with a swarm if she is still alive.

Sometimes in a case of supersedure the old queen and her newly mated daughter remain together in the colony for some time without apparent animosity, but, more often, the old queen disappears shortly before the young virgin queen mates, if not earlier. According to ROOR (1945) it is not known whether she dies a natural death or whether she is killed by the young queen or by the worker bees.

It is, of course, necessary that the process of replacement of an old queen should begin before, or very shortly after, her death as either a fertilised egg or a young female larva is required for the rearing of a new queen. Worker honeybees without a queen sometimes lay eggs in queen cell cups as well as in worker cells (BUTLER, 1954 *a*), but such unfertilised eggs give rise to males, except in the very rare cases when a female larva is produced which can develop into a queen (MACKENSEN, 1943).

Many suggestions have been made as to the factors which initiate queen supersedure, such as:—disease (FARRAR, 1947); inability to supply her colony with 'sufficient' eggs on account of old age (ROOR, 1945) or because of injury (WEDMORE, 1942); the production of an abnormally high proportion of drones (presumably from unfertilised eggs

laid in worker cells) as her store of sperm nears exhaustion (SNELGROVE, 1946); insufficiency of a secretion (queen substance) which the workers obtain by licking the queen's body and which, when the supply is adequate, inhibits both development of the workers' ovaries and queen production by them (BUTLER, 1954*b*, 1956). BUTLER (1954*b*) was able to demonstrate that in order that the worker bees of a colony shall remain inhibited in these ways they must be able to touch their queen and lick her body. Furthermore, BUTLER (1954*b*) showed that two particular mated, laying queens belonging to colonies (A and B) whose bees were in 1953 apparently rearing supersedure queens from young larvae in modified worker cells, were fully capable of preventing the rearing of such queens when the numbers of worker bees in their colonies were greatly reduced. This led him to suggest that queen supersedure is initiated by failure of a queen to produce the amount of queen substance required to inhibit the worker bees of her colony from rearing further queens.

Unfortunately, unless the bees are allowed to complete the process which they have started, there does not appear to be any way of distinguishing certainly between a colony which is rearing queens in the course of supersedure and one which is doing so preparatory to swarming, although beekeeping experience suggests that if only a small number of queens are being reared (say 1-5) it can fairly safely be assumed that swarming will not occur. It was possible, therefore, that the two colonies used in BUTLER's 1954 experiments were preparing to swarm rather than, as was supposed at the time, to supersede their queens. Consequently it was decided to repeat and extend these experiments, as opportunity occurred, with colonies which had actually completed the process of supersedure but had retained the superseded queens together with their successors. It was also decided to try to obtain experimental data on various other aspects of the supersedure process, including that of the influence of the rate of oviposition by the queen and that of injury leading to reduction in the mobility of the queen on the initiation of this process.

EXPERIMENT I. — TO DETERMINE THE ABILITY OF A 'SUPERSEDED' QUEEN TO INHIBIT WORKER HONEYBEES FROM REARING FURTHER QUEENS.

During 1954 two mated, laying queens were obtained, each of whose colonies (X and Y) had superseded them with a new queen. In each case the old queen had remained alive after her daughter had mated and started to lay, and in each colony the two queens, the old superseded one and her young successor, were living together and both were laying eggs.

From each of these colonies (X and Y) the young queens were removed, leaving the old queens. Within 24 hours the workers of colony X had modified 2 worker cells containing young larvae to form emergency queen cells. The bees of colony Y did not appear to have taken any steps to rear a new queen. Twenty-four hours later, however, an emergency queen cell was found in this colony and an additional one was present in colony X. No further queen cells appeared in either colony during the next 48 hours, after which this part of the experiment was terminated.

About three-quarters of the adult bees and almost all the brood were now removed from each colony together with the emergency queen cells produced during the first part of the experiment, the old queen being left behind in each case. Unfortunately the old queen of colony Y disappeared during the next 24 hours and was later found dead outside her hive. The old queen in colony X remained alive, however, and continued to lay a

small number of eggs (not more than 50) each day, and during the next 8 days her colony was regularly examined but no queen cells of any kind were found.

A mated, laying queen was next removed from a small colony Z and its adult worker bees were united with that part of colony X which contained the old, superseded queen, but no additional brood was given. Twenty-four hours later no queen cells could be found, but after 48 hours 2 emergency queen cells were present.

In each of these cases, therefore, in which there was definite evidence that queen supersedure had actually taken place, it was possible to demonstrate that the old queens who had been superseded were failing to inhibit the bees of their colonies from rearing further queens. Furthermore, in the case of one of these colonies (X) whose queen survived sufficiently long for further experiment, it was shown that her presence sufficed to keep a small proportion of the workers of her own colony from attempting to rear queens, but was insufficient to keep a larger group of bees, composed partly of members of her own colony and partly of bees from another colony, from so doing under similar conditions.

These results are similar to those obtained earlier (BUTLER, 1954 *b*) and support the hypothesis that queen supersedure is initiated by failure on the part of the queen of a colony to produce sufficient queen substance to satisfy her workers.

EXPERIMENT II. — TO DETERMINE THE INFLUENCE OF THE RATE OF OVIPOSITION UPON QUEEN SUPERSEDURE.

Both in the 1953 experiments (BUTLER, 1954 *b*) with the colonies (A and B) whose queens were, it was supposed but not demonstrated, being superseded, and also in the 1954 experiment (Experiment 1 above) with colonies X and Y whose queens had actually been superseded, the old queens concerned were laying very few eggs in comparison with the queens of other colonies in the same apiaries.

Now, beekeepers have long supposed that if a queen's output of eggs is 'insufficient' (there seems to be little agreement as to the standard by which such output should be judged) her bees will supersede her (e.g. Root, 1945; WEDMORE, 1942), and this might appear to explain why the old queens in the 1953 and 1954 experiments were being, or had been, superseded. However, as previously pointed out (BUTLER, 1954 *b*), it is clear that the workers of a colony do not have to come into contact with newly laid eggs in order that they shall remain inhibited from rearing new queens. If this were not so the workers of colonies in certain experiments (BUTLER, 1954 *b*) who only had access to the heads of their queens and were unable to see, touch or, probably, smell any eggs laid by them during the course of the experiments, or to have any contact with bees who had done so, would have produced emergency queen cells, which

they failed to do. However, since the queens used in these experiments certainly produced some eggs, dropping them as they were unable to place them in cells in the normal manner, it was possible that egg production by them was essential if access to their heads alone was to be capable of inhibiting small groups of worker bees from attempting to rear queens. It could for instance be argued —if one accepts the queen substance theory — that the production of queen substance on the head of a queen is dependent upon the production of eggs by her. That in fact queen substance production is associated with egg production. At the time no way of determining whether or not this is so could be devised.

However, during the summer of 1954, two marked, mated queens (p and q) who had been laying well, were found in colonies P and Q which were of moderate size and yet possessed neither eggs nor brood. Careful search showed that these were the only queens of any kind in their colonies; apparently they had stopped laying a few weeks earlier and observations indicated that neither of them were producing any eggs externally and yet there were no signs that the worker bees of their colonies had attempted to rear new queens to supersede them. As neither colony P nor Q possessed any eggs or young brood, however, their workers no longer had the material from which to rear supersedure queens. In order to find out whether they would do so, given the opportunity, a comb containing young worker larvae 12-17 hours old, but no eggs, was given to each colony. In neither case did the bees construct any queen cells during the next 4 days. Further combs containing young larvae, but no eggs, were then given to these colonies and still no queen cells appeared during the next 3 days, but the worker were reared in a normal manner.

The two queens (p and q), one of which was found late in May and the other at the end of June, were then substituted (by direct exchange without the use of a cage) for the actively laying queens of two other colonies (L and M), colonies P and Q being left without queens but with plenty of young worker larvae. At the same time all combs containing eggs were removed from colonies L and M, combs taken from other colonies and containing worker larvae being used to replace them. All 4 colonies were examined 3 days after the queens had been interchanged. No queen cells were found in L and M and the larvae were being tended normally, but 8 emergency queen cells were present in colony P and 5 in colony Q. The 2 queens were now removed from colonies L and M which were immediately given more young worker larvae. Two days later 6 emergency queen cells were found in each of these colonies. No eggs at all could be found in colonies P, Q, L or M whilst they contained queen p or q and it seems certain that neither queen laid any eggs in cells during these observations, nor dropped any.

These two non-laying, mated queens (p and q) were subsequently substituted for 3-6 days at a time for the mated, actively laying queens of normal colonies of moderate size. Queen p was introduced in this way to 5 colonies and queen q to 3. No queen cells were found in any of

the 5 colonies into which queen p was introduced, although there were ample opportunities for the bees to rear queens both from young worker larvae or from eggs left by the queens replaced by queen p. Queen q was found to be missing from the third colony 3 days after she had been introduced to it, but in neither of the 2 colonies to which she had been introduced successfully were queen cells found.

It is clear, therefore, that both these queens who, apart from the fact that they were producing no eggs, appeared to be perfectly normal, were capable of inhibiting the worker bees of moderately strong colonies (estimated 30,000-40,000 bees) from rearing supersedure queens, although, since the bees of all the experimental colonies quickly built emergency queen cells once these queens were removed thus leaving them without queens, they were obviously capable of so doing.

EXPERIMENT III. - - TO DETERMINE THE ABILITY OF VIRGIN QUEENS TO INHIBIT WORKER BEES FROM REARING QUEENS.

Since the presence in a colony of a mated queen who is not producing any eggs externally can be sufficient to inhibit the workers of her colony from rearing queens, it is interesting to determine whether the presence of a virgin queen who has not yet commenced to lay has a similar effect.

Normally any colony headed by a virgin queen, even by a very young one, no longer possesses any eggs or worker larvae, so that its worker bees are not in a position to exhibit any urge they may have to rear further queens. Therefore, during July 1954, in order to find out whether in fact the urge of the workers of such a colony to rear a supersedure queen is fully inhibited by the presence of its own virgin queen, the following experiment was carried out. Ten small colonies, each containing a virgin queen less than 7 days old, were each supplied with a comb containing eggs and young female larvae in worker cells — i.e. with the wherewithal to rear supersedure queens. Within 48 hours the workers of 5 of these colonies had constructed one or more emergency queen cells. It is clear, therefore, that virgin queens are not always capable of inhibiting the workers of their colonies from rearing queens.

EXPERIMENT IV. — TO DETERMINE THE INFLUENCE OF RESTRICTION OF A QUEEN'S MOVEMENTS ON QUEEN REARING BY THE WORKERS OF HER COLONY.

Many beekeepers (e.g. SNELGROVE, 1946) appear to believe that the worker bees of a colony will attempt to supersede their queen if she becomes injured or maimed and WEDMORE (1942) stated that loss of a fore-leg is more likely to cause supersedure than loss of a hind-leg. He stated that an injury which results in disturbance of a queen's laying power leads

her workers to supersede her and inferred that loss of a fore-leg results in loss of laying power. However, as it has already been demonstrated that some mated queens, even though they have ceased to produce any eggs externally, are capable of inhibiting the worker bees of their colonies from rearing further queens, this does not appear to be a satisfactory explanation. A possible alternative explanation 'might be that the supersedure of a maimed queen is due to loss of mobility on her part. Attempts were, therefore, made during the summer of 1954 to investigate the effects of limiting the mobility of queens.

Forty-two mated, laying queens of various strains were tethered on combs within their own colonies (by means of thin, wire leashes, each about 3 inches long, attached by loops around their waists) in such a way that although their movements became very circumscribed their workers could readily maintain full contact with all parts of their bodies.

Most of these colonies were moderately large and occupying two brood-chambers and their queens varied in age from about 2 months to over 2 years, most being about 1 year old.

Once a queen had been tethered she never, so far as could be determined, laid any more eggs in cells although she usually continued to produce and drop a few eggs throughout the experiment. The worker bees formed the usual 'courts' around their tethered queens, fed them, and frequently licked their bodies. As time went on they licked their queens more and more, as if desperately seeking some substance from their bodies, until most of the queens became highly polished.

Whenever necessary each experimental colony was supplied with a comb containing young worker larvae so that the bees always had plenty of suitable larvae from which to rear supersedure queens.

Each queen remained tethered either until her bees had constructed one or more queen cells or, in those cases where no such cells appeared, for a minimum period of 6 days.

During the June experiment the queens of 16 colonies were tethered and those of a further 19 control colonies remained untethered. During the July experiment, 10 queens were tethered, and 22 remained untethered; and during the August-September experiment, 16 queens were tethered and 23 remained untethered. Only during the June experiment did any queen cells appear in a control colony. In this experiment 15 queen cells were found in one of the control colonies.

The results obtained with the tethered queens are shown in Table I.

It is clear from these results that the bees whose queens were tethered during June built significantly more queen cells than the bees of the control colonies whose queens remained untethered ($P < 0.05$); similarly in the July, and also in the August-September, experiment queen cells appeared in significantly more of the experimental than of the control colonies ($P < 0.01$ in each case). It seems, therefore, that reduction of the mobility of a queen by tethering her does influence the rate of queen rearing by the worker bees of her colony. Furthermore, as it was noticed that the

TABLE I

INFLUENCE OF TETHERING THE QUEEN OF A COLONY ON QUEEN CELL PRODUCTION

IDENTITY of colony.	DATE of tethering.	DURATION (days) of tethering.	TIME (days) before first queen cells found.	NO. AND TYPE of queen cells found.
1	June 12th	13	None produced	—
2	June 23rd	6	4	1 emergency* (1)
3	June 23rd	6	None produced	—
4	June 23rd	6	4	1 cup with egg* (2)
5	June 23rd	6	None produced	—
6	June 23rd	6	None produced	—
7	June 23rd	6	4	1 emergency
8	June 23rd	6	None produced	—
9	June 23rd	6	None produced	—
10	June 23rd	6	None produced	—
11	June 23rd	6	6	2 emergency
12	June 23rd	7	6	4 emergency
13	June 23rd	7	None produced	—
14	June 23rd	7	None produced	—
15	June 23rd	7	None produced	—
16	June 23rd	6	2	2 cups with eggs
17	July 5th	9	None produced	—
18	July 5th	9	None produced	—
19	July 5th	9	9	6 emergency
20	July 5th	7	7	1 emergency
21	July 5th	9	None produced	—
22	July 5th	9	None produced	—
23	July 5th	14	11	3 cups with eggs
24	July 5th	9	None produced	—
25	July 5th	9	9	2 emergency
26	July 5th	9	None produced	—
27	August 3rd	24	None produced	—
28	August 16th	11	None produced	—
29	August 16th	21	None produced	—
30	August 16th	11	7	1 emergency
31	August 16th	18	15	1 cup with egg
32	August 16th	14	11	1 emergency
33	August 16th	9	None produced	—
34	August 16th	14	11	1 emergency
35	August 16th	9	7	2 emergency
36	August 16th	4	None produced	—
37	August 16th	18	None produced	—
38	August 16th	33	None produced	—
39	August 16th	18	None produced	—
40	August 16th	18	4	1 emergency
41	August 16th	18	None produced	—
42	September 1st	10	7	3 cups with eggs & 1 emergency

(1) Emergency queen cell = worker cell, containing larva, modified as a queen cell.

(2) Cup with egg = cell built as a queen cell from the start.

worker bees seemed to be licking their tethered queens much more thoroughly than the workers licked the untethered queens in the control colonies, it is very probable that they were urgently seeking some substance from their bodies which was in short supply. If the queen substance theory is correct this substance could have been queen substance, and it seems possible that the tethering of a queen in some way tends to reduce her output of this substance. If this is true one could suppose that upon being released her output of queen substance would, provided that she had not been injured by the tethering, probably soon return to about the same level as it had been before she was tethered, in which case her workers should not (according to the theory) have been any more inclined to rear new queens than they were before their queen was tethered. Data on this subject were collected and are shown in Table II.

TABLE II

FATE OF QUEEN CELLS, BUILT WHILST QUEENS WERE TETHERED, DURING THE 5 DAY PERIOD IMMEDIATELY AFTER THE QUEENS HAD BEEN UNTETHERED.

IDENTITY of colony.	CELLS destroyed by bees.	CELLS RETAINED & queens allowed to emerge.	COLONY swarmed.	COLONY superseded queen without swarming.
2	No	Yes	Yes	No
4	Yes	No	No	No
7	Yes	No	No	No
11		Colony, given special treatment after cells built.		
12	Yes	No	No	No
16	Yes, after initial increase in no:	No	No	No
19		Colony given special treatment after cells built.		
20	Yes, after initial increase in no:	No	No	No
23	Yes	No	No	No
25	Yes, after initial increase in no:	No	No	No
30	Yes	No	No	No
31	Yes	No	No	No
32		Queen died whilst tethered.		
34		Queen died whilst tethered.		
35	Yes*	No	No	No
40	Yes, before queen released.	No	No	No
42		Queen died whilst tethered.		

It will be seen that in 1 case (colony 40) the bees built only 1 emergency queen cell and subsequently destroyed it whilst their queen was still tethered. In 3 other cases the queens died whilst still tethered, and in 2 more cases the colonies were given special treatment directly their queens

(*) In this case a virgin queen emerged from 1 of the 2 emergency queen cells but she was found dead (presumed killed) about the time that the other queen cell was destroyed by the bees.

were released. In the remaining 13 cases the queens were released and the queen cells left intact by the experimenter. In 1 of these cases (colony 2) the bees swarmed with the queen less than 24 hours after she had been released; in the other 12 cases all the queen cells had been destroyed (presumably by the workers rather than by the queens) within 5 days of the queens being released (usually within 3-4 days) without swarming or queen supersedure taking place. In 3 of these cases further queen cells were built before the whole lot were destroyed.

Special treatment was given to colonies 11 and 19 when their queens were untethered. In the case of colony 11 the queen was removed and replaced by a mated, laying queen which was also tethered, and which had been taken from a non-experimental colony in which no queen cells were present. Within 24 hours both the emergency queen cells had been destroyed. The queen in colony 19 was also replaced by a mated, laying queen from a non-experimental colony without queen cells, with similar results.

Two further points about the data in Table I are worth noting: — First, that in 5 out of 17 cases in which colonies attempted to rear queens, eggs appeared in queen cell cups—i.e. cells especially built as queen cells from their inception. Since the tethered queens could not reach these cups in order to oviposit in them, the worker bees must either have carried eggs dropped by queens and placed them in the cups or else the workers must themselves have laid them in the cups. Of these two possibilities the former appears to be much the more probable as none of the signs typical of the presence of "laying workers" were found. Secondly, that if one compares the proportion of colonies in which queen cells were built, within 6 days of their queens being tethered, in the different months, one finds that the proportion in June was significantly greater ($P < 0.01$) than that in July and August together. This may perhaps indicate that queen cell production is more likely to occur in the former period than in the latter.

DISCUSSION

FARRAR (1947) has described a number of instances in which the worker bees of colonies, the queens of which were infected with *Nosema* disease, were replacing their queens, and he considered these to be cases of queen supersedure. However, since he found emergency queen cells present in these colonies rather than queen cell cups in which the queens being replaced had laid eggs, and, further, since these emergency queen cells were found shortly after, rather than before, the queens had either died or become moribund, it would seem better to regard these as cases in which the worker bees were making emergency preparations to replace queens who had suddenly died—in the same way as they would have done had their queens been healthy and been suddenly removed by the beekeeper—rather than as cases of queen supersedure as defined in the introduction

to this paper. There does not, indeed, appear to be any reliable evidence which shows that diseased queens are likely to be superseded by their workers, although it seems possible that they are.

The results of Experiment II support the conclusion of Butler (1954 *b*) that neither laying of eggs in cells by a queen, nor indeed their production externally, are necessary to enable her to inhibit a colony from producing queen cells. Thus the hypotheses of Root (1945) and WEDMORE (1942) that supersedure of old or injured queens is initiated by their inability to produce a sufficient number of eggs are no longer tenable. It also seems clear that the poor ability of virgin queens to inhibit queen production by worker bees as demonstrated in Experiment III, cannot be explained by the fact that they are not in an egg-laying condition.

The suggestion that queen supersedure is initiated by the worker bees of a colony becoming aware that their queen is laying unfertilised eggs on account of near exhaustion of her store of sperm (Snelgrove, 1946) is clearly invalid, as a number of cases have occurred at Rothamsted in which both naturally mated and instrumentally inseminated queens have become partial or complete drone-layers (i.e. come to lay unfertilised, drone-producing eggs in worker cells). Despite this the bees of their colonies made no attempts to rear new queens. In fact, as Mackensen (1951) showed, it is possible by treating queens with carbon dioxide to cause them to lay eggs without insemination, and such queens appear to be fully capable of inhibiting the workers of their colonies from attempting to rear further queens.

Butler (1954 *b*) showed that a substance which the worker bees obtain by licking the body their queen is fully capable of inhibiting them from rearing further queens. He further demonstrated that the larger the number of worker bees the greater the amount of this queen substance necessary to inhibit them from queen rearing. In Experiment I a queen which had actually been superseded by her bees, but still remained alive, was shown to be capable of inhibiting queen rearing in small colonies but not in large ones. It seems fairly certain, therefore, that she had been superseded because her production of queen substance was insufficient to inhibit queen rearing in her own colony. It is, likely, therefore, that a shortage of queen substance is the only immediate cause of queen supersedure, and that disease and injury produce their effects, if any, by reducing the ability of a queen to produce sufficient queen substance.

The production of queen cells by colonies whose queens were tethered (Experiment IV) also suggests that a queen's output of queen substance is reduced by limiting her mobility, though this reduction is only temporary and ceases, though sometimes not immediately, when she is released. Injury to a queens' limbs may, therefore, perhaps lead to her supersedure by limiting her powers of movement.

Whilst it seems fairly certain that the supersedure of any queen is directly due to inadequacy in her output of queen substance, it also seems probable that the immediate cause of queen production in colonies prepa-

ring to swarm is also due to lack of inhibition by queen substance. Unfortunately the interrelationships between the processes of queen supersedure and swarming are still far from clear.

Summary.

1. The process known as 'queen supersedure' in honeybee colonies is defined. It involves queen rearing by worker bees in the presence of their old queen, without the emergence of a swarm.

2. Many suggestions have been made to account for this process. It has, for example, been suggested that it is initiated by:

(a) the worker bees becoming aware that their queen, either on account of old age or injury, is failing to produce 'sufficient' eggs;

(b) the worker bees becoming aware that their queen is laying unfertilised eggs in worker cells as her supply of sperm fails;

(c) the queen becoming diseased;

(d) failure of the queen to produce sufficient queen substance to inhibit the workers from rearing further queens.

Each of these suggestions has been investigated.

3. It is demonstrated that non-production of eggs externally by a queen does not prevent her from inhibiting her workers from rearing further queens; therefore hypothesis (a) fails. Nevertheless it was found that young virgin queens do not always inhibit queen rearing by the workers of their colonies. This cannot be explained by the fact that they are producing no eggs.

4. Queens which are laying unfertilised, drone-producing, eggs in worker cells are often capable of inhibiting worker bees from rearing queens, therefore hypothesis (b) is invalid.

5. It is demonstrated that a queen, which had actually been superseded by her workers, was capable of inhibiting queen rearing in small, but not in large colonies. Since it has been shown that a substance which workers obtain from their queens (queen substance) inhibits them from rearing further queens, provided that the quantity is sufficient for the number of bees present in their colonies, it is probable that this queen was producing insufficient queen substance to inhibit queen rearing in a large colony.

6. It is concluded that shortage of queen substance is the only *immediate* cause of queen supersedure, and that any other factors which tend to cause queen supersedure do so by reducing her production of queen substance.

7. Reducing the mobility of queens, by tethering, frequently leads to queen cell production so long as the tethering is continued, thus suggesting that any effects of injury or disease may be attributed to their interference with the mobility of the queen and lead to a reduction in her queen substance output.

Résumé.

1. L'auteur définit le processus de biologie apicole connu sous le nom de « queen supersedure ». Il consiste dans l'élevage d'une reine par des ouvrières en présence de leur vieille reine, sans sortie d'un essaim.

2. On suggère quatre possibilités de déclencher le processus :

a) les ouvrières ont connaissance du fait que leur reine, soit à cause de son âge, soit par accident, ne peut plus pondre d'œufs en nombre « suffisant » ;

b) les ouvrières ont connaissance du fait que leur reine pond des œufs stériles dans les cellules d'ouvrières parce qu'elle n'a plus de réserve de sperme ;

c) la reine devient malade ;

d) la reine est dans l'impossibilité de produire une quantité suffisante de « queen substance », qui inhibe l'élevage d'autres reines par les ouvrières.

Chacune de ces suggestions a été envisagée successivement.

3. On démontre que la réduction de la ponte d'une reine ne peut pas l'empêcher d'inhiber l'élevage de nouvelles reines par les ouvrières ; ainsi tombe l'hypothèse *a*. Toutefois, on sait que les jeunes reines vierges n'inhibent pas toujours l'élevage de reines par les ouvrières de la colonie. Ceci ne peut pas s'expliquer par le fait qu'elles ne pondent pas d'œufs.

4. Les reines non fécondées qui pondent des œufs produisant des bourdons dans les cellules d'ouvrières sont souvent capables d'inhiber l'élevage des reines par les ouvrières, ce qui invalide l'hypothèse *b*.

5. On démontre qu'une reine qui vient d'être élevée par ses ouvrières est capable d'inhiber l'élevage dans les petites colonies mais pas dans les grandes. Puisqu'on a démontré qu'une substance que les ouvrières obtiennent de leurs reines (« queen substance ») inhibe les capacités d'élever de futures reines et que la quantité de substance est proportionnelle au nombre d'individus dans la ruche, il est probable que cette jeune reine ne produit pas assez de « queen substance » pour une grande colonie.

6. On conclut que la diminution de la « queen substance » est la seule cause immédiate du départ de l'élevage. Les autres facteurs agissant dans le même sens en définitive réduisent d'abord la production de « queen substance ».

7. La réduction de mobilité de la reine induit la construction de cellules royales aussi longtemps que dure la réduction ; ceci suggère que les effets des blessures ou des maladies peuvent amener une diminution de la quantité de substance distribuée en agissant sur les déplacements de la reine.

Zusammenfassung.

1. Der Vorgang der „Stillen Umweiselung“ im Bienenvolk wird definiert. Er besteht darin, daß die Arbeitsbienen in Gegenwart der alten Königin ohne Schwarmbildung einen neuen Weisel heranzüchten.

2. Viele Vorschläge sind schon gemacht worden, um diesen Vorgang zu erklären. Es wurde zum Beispiel vorgeschlagen, daß er folgendermassen hervorgerufen wird :

a) die Arbeiterinnen werden gewahr, daß ihre Königin, entweder wegen zu hohen Alters oder Verletzung, nicht mehr imstande ist, genügend Eier zu legen ;

b) die Arbeiterinnen stellen fest, daß ihre Königin, unbefruchtete Eier in Arbeiterinnenzellen legt, da der Samenvorrat erschöpft ist ;

c) die Königin ist von einer Seuche befallen worden ;

d) die Königin ist nicht fähig, eine genügende Menge Königinsubstanz zu erzeugen, um die Arbeitsbienen an der Zucht weiterer Königinnen zu hindern.

3. Es wurde bewiesen, daß das Ausbleiden der äußerlichen Eiablage durch die Königin sie nicht davon abhält, die Arbeiterinnen an der Zucht weiterer Königinnen zu hindern ; daher kann die erste Hypothese (*a*) als ungültig betrachtet werden. Es wurde jedoch festgestellt, daß junge, unbegattete Königinnen nicht immer in ihren Völkern die Zucht von Königinnen durch Arbeiterinnen verhindern. Dies kann nicht durch die Tatsache erklärt werden, daß sie keine Eier legen.

4. Königinnen, die unbefruchtete Eier, aus denen Drohnen schlüpfen, in Arbeiterinnenzellen legen, sind oft fähig, Arbeitsbienen an der Königinnenzucht zu hindern ; daher trifft Hypothese (*b*) nicht zu.

5. Es wird bewiesen, daß eine Königin, die tatsächlich von den Arbeitsbienen umgeweiselt wurde, fähig war, Königinnenzucht in kleinen, nicht aber in großen Völkern zu verhindern. Da es aber schon bewiesen worden ist, daß eine Substanz, die die Arbeiterinnen von ihrer Königin erhalten (Königinsubstanz) die Zucht weiterer Königinnen verhindert, vorausgesetzt daß eine genügende Menge vorhanden ist, um

die Arbeitsbienen des ganzen Volkes zu versorgen, ist es wahrscheinlich, daß diese Königin ungenügende Mengen dieser Königinsubstanz erzeugte, um die Weiselzucht in einem grossen Volk zu unterdrücken.

6. Es wird die Folgerung gezogen, daß Mangel an Königinsubstanz der einzige unmittelbare Grund für die stille Umweiselung ist, und daß alle anderen Faktoren die dazu neigen, die stille Umweiselung hervorzurufen, insofern mitwirken, indem sie die Erzeugung von Königinsubstanz reduzieren.

7. Behinderung der Beweglichkeit der Königin durch Anbinden führt häufig zum Bau von Weiselzellen, solange die Königin ihrer Freiheit beraubt ist, was darauf hindeutet, daß Verletzung oder Seuche sich in Beweglichkeitsbehinderung der Königin auswirken und zur Reduktion der Königinsubstanzabgabe führen.

I wish to take this opportunity to thank my friend Dr. J. Simpson for many helpful suggestions during the course of this work and especially for his advice during the preparation of this paper for publication.

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ZUCKERABBAU UNTER DER EINWIRKUNG DER INVERTIERENDEN FERMENTE IN PHARYNXDRÜSEN UND MITTELDARM DER HONIGBIENE

(*APIS MELLIFICA* L.) (1) (2)

I. SOMMERBIENEN DER KRAINER- UND NIGRA-RASSE

von

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INHALT:

1. EINLEITUNG UND FRAGESTELLUNG.
2. VERSUCHSANORDNUNG UND METHODIK.
3. ERGEBNISSE DER UNTERSUCHUNGEN.
 - a. Verlauf der Hydrolyse der geprüften Zuckerarten.
 - b. Wirkung der Pharynxdrüsen- und Mitteldarmextrakte.
 - c. Einfluß der Ernährung und des physiologischen Zustandes der Bienen auf die Wirkung der Extrakte.
 - d. Unterschiede der Fermentwirkung zwischen Krainer- und Nigrabienen.
4. DISKUSSION DER ERGEBNISSE.
5. ZUSAMMENFASSUNG.
6. LITERATUR.

I. EINLEITUNG UND FRAGESTELLUNG

Die Honigbiene sammelt in der umgebenden Pflanzenwelt zuckerhaltige Rohstoffe, die ihr einerseits zur individuellen Ernährung, anderseits zur Anlage von Vorräten dienen. Die Rohstoffe, Nektar und Honigtau, enthalten eine Anzahl von Kohlehydraten, die während der Verdauung und der Einlagerung in den Wabenzellen, unter der Einwirkung invertierender Fermente weitgehende chemische Umwandlungen erfahren. Als Bestandteile von Nektar und Honigtau sind folgende Kohlehydrate festgestellt worden: Fruktose, Glukose, Saccharose, Maltose, Isomaltose, Fruktomaltose, Maltotriose, Maltotetraose, Impatiöse, Melezitose, Melibiose, Raffinose, Panose, Dextrine, Dulcitol, Mannit, Inosit, Ribitol und eine Reihe nicht näher identifizierter Oligosaccharide (BARTELS, BEUTLER, BEUTLER und WAHL, BONNIER, DUSPIVA, 1953, 1954 *a* und *b*, v. FELLENBURG, FREY, ZIMMERMANN und MAURIZIO, GEINITZ, GORBACH, GRAY, GRAY und FRÄNKEL, 1953, 1954, MAURIZIO, 1954 *a* und *b*, MICHEL, NOTBOHM und LUCIUS, v. PLANTA, TÄUFEL und REISS, WYKES, 1952, ZIMMERMANN, 1952, 1953, 1954).

Nach bisherigen Untersuchungen kommen Karbohydrasen (Diastase, Invertase) vor allem in zwei Organen der Honigbiene vor, in den Pharynxdrüsen und im Mitteldarm (EVENIUS, GONTARSKI, 1954, KOSMIN und KOMAROV, KRATKY, SARIN); in den Pharynxdrüsen wird außerdem eine Oxydase abgesondert (GAUHE, GONTARSKI, 1948). Es wird angenommen, daß die Bienendiastase und -invertase identisch sind; dagegen

(1) Herrn Prof. Dr. K. v. Frisch zum 70. Geburtstag gewidmet.

(2) Vorläufige Mitteilung in *Bee World*, 1957, **38** (1) : 14.

scheinen zwischen den Fermenten der Pharynxdrüsen und des Mitteldarmes Unterschiede zu bestehen (GONTARSKI, 1954). Ein unterschiedliches Verhalten wurde auch zwischen den Fermenten verschiedener Bienenrassen festgestellt (GONTARSKI, 1953). Die Honiginvertasen gelangen zum größten Teil aus dem Pharynxdrüsensekret der Bienen während der Verarbeitung in die reife Honigmasse; zu einem geringeren Teil stammen sie aus den Rohstoffen selbst (BEUTLER, 1953, BEUTLER und WAHL, BONNIER, DUSPIVA, 1953, 1954 b, FREY, ZIMMERMANN und MAURIZIO, MAURIZIO, 1954 b, ZIMMERMANN, 1953, 1954).

Die Methode der Papierchromatographie bietet neue Möglichkeiten für die Untersuchung enzymatischer Vorgänge. Vor allem erlaubt sie einen exakten Nachweis der während der Hydrolyse entstehenden Abbauprodukte. Da ich seit mehreren Jahren mit papierchromatographischen Untersuchungen an Nektar und Extrakten aus Pharynxdrüsen von Bienen beschäftigt bin, interessierten mich die oben aufgeworfenen Fragen ganz besonders. Ich unternahm deshalb im vergangenen Jahr eine qualitative papierchromatographische Untersuchung, welche in Ergänzung der bisher bekannten Tatsachen, vor allem eine Abklärung folgender Fragen zum Ziel hatte: 1. Welche Zuckerarten werden von den Bieneninvertasen hydrolysiert und wie geht der Abbau vor sich? — 2. Bestehen Unterschiede der Wirkung zwischen dem Mitteldarm- und dem Pharynxdrüsenferment? — 3. Welchen Einfluß üben Ernährung und physiologischer Zustand der Bienen auf die Wirkung der invertierenden Fermente aus? — 4. Bestehen Unterschiede der Fermentwirkung zwischen Bienen der Krainer- und Nigra-Rasse?

2. VERSUCHSANORDNUNG UND METHODIK

BIENENMATERIAL.

Sollen in physiologischen Arbeiten zuverlässige Resultate erzielt werden, ist es wichtig, Bienen bekannten Alters und bekannter Herkunft zu verwenden. Ich arbeitete stets mit Sommer-Jungbienen, die im Thermostaten aus Brutwaben geschlüpft waren. Die höchstens 24 Stunden alten Bienen wurden zum Teil gezeichnet und in Völkern des Liebefelder Standes zugesetzt, zum Teil in Liebefelder Käfigen eingeschlossen, mit Zuckerteig (1) oder mit einer Mischung von Zuckerteig und Pollen (1) gefüttert und im Zuchtthermostaten (30° C) gehalten. 21 Tage nach Versuchsbeginn wurden die Bienen aus Völkern und Käfigen entnommen, mit Chloroform getötet und zur Gewinnung von Extrakten verarbeitet. Bei der Präparation wurden die Pharynxdrüsen auf ihren Entwicklungsgrad eingeschätzt. Die Versuche wurden in je zwei Wiederholungen, in Parallelserien mit Bienen der braunen, schweizerischen Landrasse (im folgenden als „Nigra“ bezeichnet) und einer Nachzucht von Krainerköniginnen jugoslawischer Herkunft (als „Krainer“ bezeichnet) geführt (2).

HERSTELLUNG DER EXTRAKTE.

a) *Pharynxdrüsenextrakt*. — Die Pharynxdrüsen der Bienen wurden herauspräpariert (Methode s. MAURIZIO, 1954, c) und in sterilisierten Wägegläsern in steriles, destilliertes Wasser eingelegt, im Verhältnis von 10 Bienen (20 Drüsen) auf 1 ccm Wasser, d. h. 1 Tiereinheit auf 0,1 ccm Extrakt. Die Wägegläsern wurden über Nacht (18—20

(1) Zuckerteig = 2 Gewichtsteile Honig + 5 Gewichtsteile Staubzucker. Zuckerteig-Pollenmischung = Zuckerteig mit 15 prozentiger Beigabe frischer, mit der Pollenfalle gesammelter, nicht nach Herkunft sortierter Pollenhörschen.

(2) Die Bienen der Landrasse stammten in einem Versuch aus einem Volk des Liebefelder Standes, im andern vom Stand *H. Schneider*, Jens (Stamm « Martha »); die Krainer-Bienen in beiden Versuchen vom Stand *Schneider*. Bei letzteren handelt es sich um eine Nachzucht von Krainerköniginnen jugoslawischer Herkunft, deren Tochterköniginnen auf einer drohnensicheren Gebirgsbelegstation mit Drohnen derselben Herkunft begattet wurden. Die Nachkommenschaft wurde anhand der Rassemkmale selektioniert.

Stunden) im Thermostaten (30° C) gehalten. Danach wurden die Extrakte durch sterilisierte Papierfilter und flambierte Trichter in sterile Serumröhrchen filtriert und mit sterilen Pipetten im Verhältnis von 0,5 ccm Extrakt mit 1 ccm Zuckerlösung gemischt.

b. *Darmextrakte*. — Der Darm wurde auf übliche Weise, am letzten Abdominalsegment mit einer Pincette gefaßt und aus dem Abdomen gezogen. In der Luft hängend wurde die Honigblase mit einer Schere abgeschnitten; ein zweiter Schnitt trennte den Mittel- und Dünndarm von der Kotblase, wobei der Mitteldarm in ein Uhrsälchen mit sterilem, destilliertem Wasser fiel. Hier wurden die Malpighischen Gefäße vom Mitteldarm gelöst, nach hinten gestrichen und durch einen Schnitt, samt dem Dünndarm entfernt (Methodik s. EVENIUS, GONTARSKI, 1954). Dabei tritt der Großteil des Darminhaltes aus, der Rest wurde durch bestreichen mit einer Pincette aus dem Darmlumen entfernt. Der leere Mitteldarm wurde in ein zweites Uhrsälchen mit sterilem Wasser gelegt, von eventuell anhaftenden Inhaltsresten befreit und in einem dritten Schälchen nachgespült. Darauf wurden die leeren Darmschläuche in einem ausgeflamten Mörser in einigen Tropfen sterilen, destillierten Wassers zerrieben und in sterile Wägegläschen abgespült im Verhältnis von 2 Därmen auf 1 ccm Wasser, d. h. 1 Tiereinheit auf 0,5 ccm Extrakt. Ich arbeitete demnach mit Extrakten der Darmwand und nicht mit solchen des Darminhaltes. Die Darmextrakte wurden weiterhin wie die Drüsenextrakte behandelt, d. h. im Thermostaten gehalten, nach 18—20 Stunden filtriert und im Verhältnis von 0,5 ccm Extrakt mit 1 ccm Zuckerlösung gemischt.

ZUCKERLÖSUNGEN.

Das Hydrolyisierungsvermögen der Drüsen- und Darmextrakte wurde an folgenden 8 Zuckerarten geprüft: Saccharose, Maltose, Trehalose, Lactose, Melezitose, Melibiose, Raffinose und Dextrin, d. h. vier Disaccharide, drei Trisaccharide und ein Polysaccharid. Die verwendeten Zucker waren chemisch reine Produkte der Firmen E. MERCK, Darmstadt, und G. T. GURR Ltd., London. Von den 8 Zuckerarten wurden mit sterilem, destilliertem Wasser 20-prozentige Lösungen hergestellt. Nach Mischung mit den Extrakten enthielten die Lösungen 133 mg Zucker pro 1 ccm. Die Verdünnung der Drüsen- und Darmextrakte und die Konzentration der Zuckerlösungen wurden nach Vorversuchen mit Saccharose so gewählt, daß sich im Chromatogramm ein optimales Bild des Zuckerabbaus ergab. Zur Verhütung von Pilzinfektionen wurde den Zuckerlösungen 1 ‰ Nipagin beigegeben. Diese Menge genügt, um ein Schimmeln der Zucker-Extraktlösungen während längerer Zeit (3—4 Monate) zu verhindern. Voraussetzung dafür ist, daß sowohl die Extrakte, wie die Zuckerlösungen bei der Verarbeitung möglichst steril behandelt werden. Von einer Hitzesterilisierung der Zuckerlösungen sah ich ab, um eine Hitzehydrolyse zu vermeiden, die sich im Chromatogramm störend auswirken könnte.

PAPIERCHROMATOGRAPHISCHE VERARBEITUNG.

Vorversuche hatten gezeigt, daß die Hydrolyse der einzelnen Zuckerarten sehr verschieden schnell vor sich geht. Um diesen Umstand zu berücksichtigen, wurden die im Thermostaten gehaltenen Extrakt-Zuckerlösungen in verschiedenen Zeitabständen auf Chromatographiepapier gebracht, nämlich 24 Stunden, 3, 10 und 21 Tage nach der Mischung. Für Lactose und Melibiose wurden weitere Chromatogramme nach 3 Monaten angefertigt. Um ein Eintrocknen der Lösungen zu vermeiden, wurden die Serumröhrchen mit steriler Watte und Gummistopfen verschlossen.

Für die Chromatogramme wurde Papier Whatman 1 verwendet. Die Trennung erfolgte im absteigenden Verfahren mit dem n-Butanol-Essigsäure-Wasser-Gemisch (4 : 1 : 5) und einer Durchlaufzeit von 3,5 bis 4 Tagen. Zur Kontrolle wurden neben den Extrakt-Zuckerlösungen jeweils reine Lösungen der geprüften Zuckerarten und reine Extrakte auf das Papier gebracht. Bei letzteren konnten nie Spuren von Zucker nachge-

wiesen werden. Die Lösungen wurden mit geeichten Kapillarpipetten auf das Papier aufgetragen. Die Entwicklung der Chromatogramme erfolgte mit einer 1-prozentigen alkoholischen Lösung von p-Anisidin-Hydrochlorid. Die gespritzten, luftgetrockneten Chromatogramme wurden in einem in Liebefeld gebauten, elektrischen Heizofen bei 110—120° C entwickelt. Der, nach einem Entwurf von Dr. P. RITTER, von der Firma L. EGERTER, Liebefeld, gebaute Ofen hat sich gut bewährt, weil darin die ganze Fläche der Chromatogramme gleichmässig erhitzt wird und der Entwicklungsvorgang durch eine Scheibe direkt verfolgt werden kann (Abb. 1).

Mit p-Anisidin-Hydrochlorid werden alle geprüften Zuckerarten und ihre Abbau-
produkte sichtbar gemacht, mit Ausnahme von Trehalose. Diese wird zwar mit Anisidin,
wie auch mit andern Spritzlösungen (z. B. Anilinphthalatsäure, Vanillin usw.),
entwickelt, erschien jedoch bei den von mir verwendeten Mengen nur sehr schwach

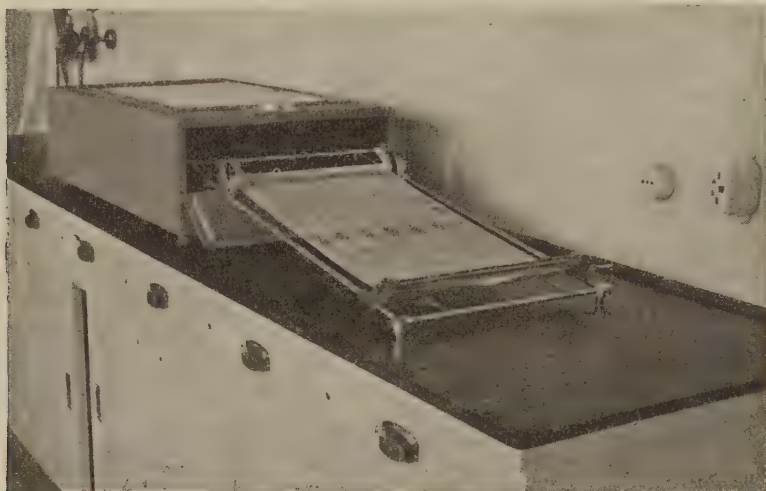


Abb. 1. — Liebefelder Entwicklungsgerät für Papierchromatogramme (im herausgezogenen Rahmen eingespanntes Chromatogramm).

oder gar nicht in den Chromatogrammen. Ich verzichtete deshalb in der Folge auf eine Sichtbarmachung der Trehalose und begnügte mich mit dem Nachweis der aus ihrer Aufspaltung entstehenden Glukose (Abb. 6).

Die Chromatogramme wurden nur qualitativ ausgewertet. Da jedoch in allen Versuchen die gleichen Zuckerlösungen, in gleicher Mischung mit den auf gleiche Weise gewonnenen Extrakten Verwendung fanden und die Methodik der Papierchromatographie stets dieselbe war, erlauben sie bis zu einem gewissen Grade auch eine quantitative Beurteilung des Spaltungsvorganges.

Für die gute Zusammenarbeit und die zuverlässige Ausführung der technischen chromatographischen Arbeiten möchte ich hier Frl. M. ZUBERBÜHLER den besten Dank aussprechen; für die Beschaffung des Bienenmaterials und die Ausführung der mit den Versuchen verbundenen bienenzüchterischen Arbeiten bin ich den Herren A. BRÜGGER und H. SCHNEIDER zu Dank verpflichtet. Alle Photographien von Chromatogrammen wurden von Frl. H. KOLLMANN ausgeführt, wofür ihr bestens gedankt sei.

3. ERGEBNISSE DER UNTERSUCHUNGEN

a. VERLAUF DER HYDROLYSE DER GEPRÜFTEN ZUCKERARTEN.

Von den 8 geprüften Zuckerarten wurden 6 von allen Extrakten hydrolysiert. Am schnellsten ging der Abbau bei Maltose und Saccharose vor sich, etwas langsamer verlief er bei Trehalose, Melezitose, Raffinose und Dextrin. Lactose und Melibiose zeigten in den ersten drei Wochen nach Versuchsbeginn keine Anzeichen einer Hydrolyse. Erst in den nach 3 Monaten angesetzten Chromatogrammen erschienen bei Melibiose schwache Flecke von Abbauprodukten, während bei Lactose auch nach dieser Zeitspanne keine Hydrolyse stattfand.

Bei der Mehrzahl der geprüften Zuckerarten fand gleichzeitig mit der Abspaltung von Monosacchariden, eine Synthese höhermolekularer Oligosaccharide statt. So entstanden z. B. während der Hydrolyse von *Maltose* und *Saccharose*, neben Glukose, resp. Glukose und Fruktose, 3—5 weitere, in den Chromatogrammen oberhalb der Maltose lokalisierte Saccharide mit niedrigen R_F -Werten (Abb. 2, 3, 8, 9). Eine solche, während der Hydrolyse durch Gruppenübertragung stattfindende Synthese von Oligosacchariden ist in den letzten Jahren für zahlreiche pflanzliche und tierische Fermente nachgewiesen worden (ARONOFF und BACON, BACON, 1952, 1954 *a* und *b*, BACON und EDELMAN, 1950, 1951, BEALING und BACON, BLANCHARD und ALBON, DUSPIVA, 1953, 1954 *a* und *b*, EDELMAN und BACON, 1951 *a* und *b*, MAURIZIO, 1954 *a*, PAZUR und FRENCH, WALLENFELS und MITARBEITER, 1952, 1953, WHITE, WHITE und MAHER, 1952, 1953, ZIMMERMANN, 1953, 1954, dort weitere Literatur).

Auch während der Hydrolyse von Melezitose und Raffinose bildete sich neben niedermolekularen Abbauprodukten oft ein höhermolekulares Saccharid (Abb. 4, 5, 10). Die *Melezitosespaltung* verlief stets unter Bildung von Fruktose und Glukose; in einzelnen Chromatogrammen fand sich außerdem ein auf der Höhe der Saccharose lokalisierter, offenbar der Turanose entsprechender Fleck (Abb. 4, 10). Die Entstehung von Turanose als Zwischenstufe des Melezitoseabbaus durch die Bienenfermente ist insofern interessant, als unter der Wirkung der Honiginvertase und der Darmfermente von Aphiden. Melezitose direkt zu Fruktose und Glukose, ohne Bildung von Turanose abgebaut wird (DUSPIVA, 1954 *b*, WHITE und MAHER, 1953). Als Produkte der *Raffinosespaltung* erschienen in der Mehrzahl der Chromatogramme Flecke von Melibiose und Fruktose; in einzelnen trat außerdem ein schwacher Glukosefleck auf, was auf einen teilweisen Abbau der Melibiose hinweist (Abb. 5). Ähnlich wird von WHITE und MAHER (1953) der Raffinoseabbau unter dem Einfluß der Honiginvertase beschrieben, während nach DUSPIVA (1954 *b*) Aphidenextrakte Raffinose direkt zu Glukose und Fruktose, ohne Melibiosebildung, abbauen. In den Serien mit *Trehalose* trat Glukose als einziges Abbauprodukt auf (Abb. 6).

Abb. 2—6. — Papierchromatogramme der Zucker-Hydrolyse unter der Wirkung von Mitteldarm- und Pharynxdrüsenextrakten von Bienen aus dem freiliegenden Volk.

V = Vergleichszuckerreihe ; A = Darmextrakte ; B - Drüsenextrakte ; K - Kräpferbienen ; N = Nigrabienen.



Abb. 2. — Saccharose-Abbau, Papierchromatogramme 3 Tage nach Versuchsbeginn.

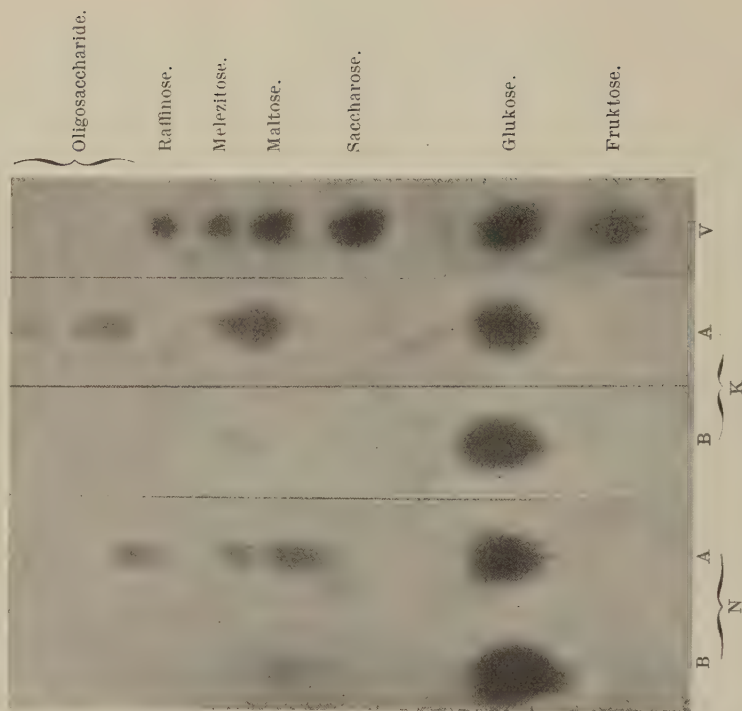


Abb. 3. — Maltose-Abbau, Papierchromatogramme 3 Tage nach Versuchsbeginn.

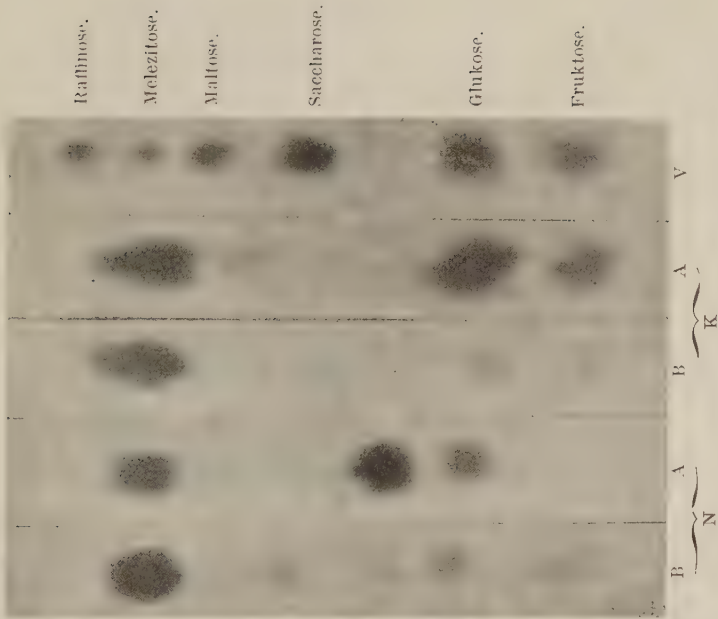


Abb. 4. — *Melezitose*-Abbau, Papierchromatogramme
21 Tage nach Versuchsbeginn.

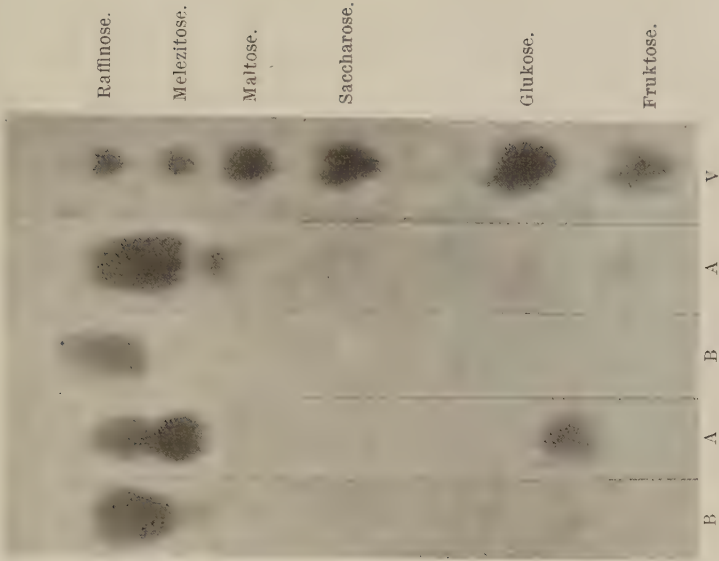


Abb. 5. — *Raffinose*-Abbau, Papierchromatogramme
21 Tage nach Versuchsbeginn.

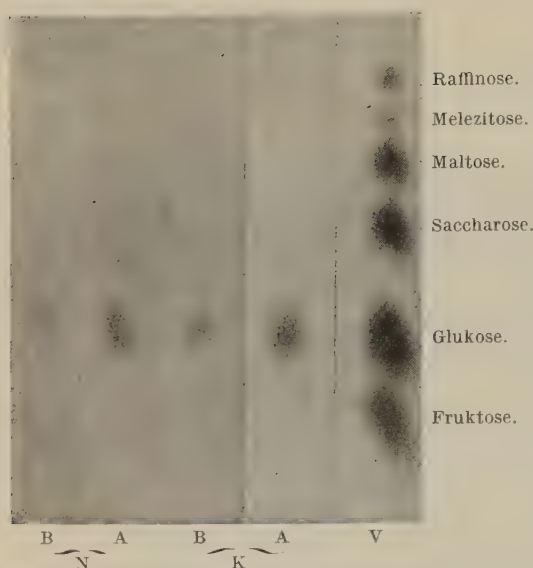


Abb. 6. — *Trehalose*-Abbau, Papierchromatogramme 21 Tage nach Versuchsbeginn.

R_F -Werten sichtbar werden. Unter dem Einfluß der Bienenfermente verändert sich jedoch das chromatographische Bild indem der Glukosefleck stark zunimmt und mehrere, im Ausgangsmaterial fehlende oder schwach vertretene höhermolekulare Saccharide erscheinen (Abb. 7).

In den *Melibiose*-Serien machten sich, wie schon weiter oben erwähnt wurde, die ersten Anzeichen einer Spaltung erst nach 3 Monaten bemerkbar. Sie äußerten sich im Auftreten schwacher, der Galaktose und Glukose entsprechender Doppelflecke, und eines weiteren, auf der Höhe der Maltose lokalisierten Saccharids.

b. WIRKUNG DER PHARYNXDRÜSEN- UND MITTELDARMEKSTRAKTE.

In der Mehrzahl der ausgeführten Versuchsserien waren Unter-

Dextrin wurde von allen Extrakten unter Anreicherung von Glukose hydrolysiert, wobei gleichzeitig schwächere Flecke von Maltose und Oligosacchariden in den Chromatogrammen auftraten (Abb. 7). Bei der Beurteilung der Dextrinhydrolyse im Chromatogramm muß man vorsichtig vorgehen und stets das chromatographische Bild des unabgebauten Ausgangsmaterials zum Vergleich heranziehen. Dextrine enthalten schon vor dem enzymatischen Abbau eine Reihe von Kohlehydraten, die im Chromatogramm als eine Kette von Flecken mit niedrigen

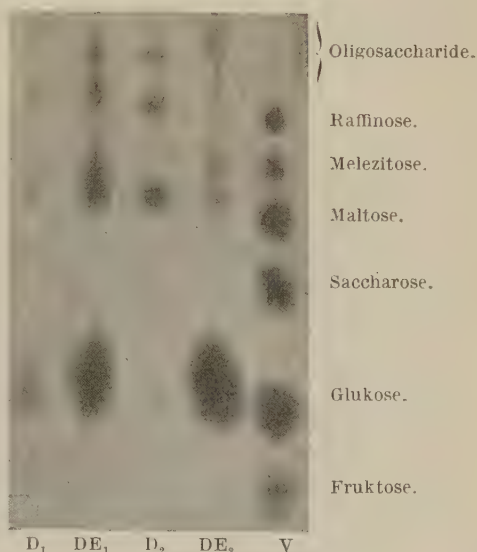


Abb. 7. — Abbau von *Dextrinen* unter der Wirkung des Pharynxdrüsenfermentes von Bienen aus dem Volk. Chromatogramm 3 Tage nach Versuchsbeginn; Nigrabienen.

V = Vergleichszuckerreihe; D_1 , D_2 = Lösungen der Dextrinpräparate 1 und 2, vor der Mischung mit dem Extrakt; DE_1 , DE_2 = Dextrinlösungen mit Extrakt.

schiede des Hydrolysierungsvermögens zwischen Pharynxdrüsen- und Mitteldarm-Extrakten festzustellen. Saccharose und Maltose wurden von den Drüsenextrakten schneller und stärker abgebaut als von den Darmextrakten; die Darmextrakte wirkten dagegen im allgemeinen stärker auf Melezitose, Raffinose und Trehalose. Auch Melibiose scheint, soweit die sehr schwache Spaltung eine Beurteilung erlaubt, vom Darmextrakt stärker angegriffen zu werden (Tab. 1).

TABELLE 1

HYDROLYSIERUNGSVERMÖGEN DER PHARYNXDRÜSEN- UND MITTELDARMEXTRAKTE GEGENÜBER DEN GEPRÜFTEN ZUCKERARTEN (MITTELWERTE ALLER SERIEN).

BIENEN		FUTTERART.	ENTWICKLUNGS- GRAD DER PHA- RYNXDRÜSEN (1).	EXTRAKT.	ZUCKERARTEN (2).							
Rasse.	Her- kunft.				Saccharose.	Maltose.	Lactose.	Trehalose.	Melezitose.	Melibiose.	Raffinose.	Dextrin.
Krainer.	Volk.			Darm. . . .	3	3	0	2	3	1	3	2
—	—		2,52	Drüsen. . .	4	4	0	1	2	?	1	2
Nigra.	—			Darm. . . .	3	3	0	2	3	1	3	2
—	—		3,10	Drüsen. . .	4	4	0	1	2	?	1	2
Krainer.	Käfig.	Zuckerteig.		Darm. . . .	3	3	0	0	1	?	1	1
—	—	—	1,10	Drüsen. . .	3	3	0	2	2	0	?	1
—	—	+ Pollen.		Darm. . . .	3	3	0	2	2	?	2	2
—	—	—	2,95	Drüsen. . .	4	4	0	2	1	0	2	3
Nigra.	—	Zuckerteig.		Darm. . . .	2	2	0	1	1	?	1	1
—	—	—	1,00	Drüsen. . .	3	3	0	?	2	0	?	1
—	—	— — Pollen.		Darm. . . .	3	3	0	2	3	?	3	2
—	—	—	3,15	Drüsen. . .	4	4	0	1	2	0	?	3

(1) Einschätzung des Entwicklungsgrades der Pharynxdrüsen s. *Maurizio* 1954 c.
 (2) Abbaustufen : 4 = sehr gut ; 3 = gut ; 2 = mittelgut ; 1 = gering ; ? = sehr gering ;
 0 = kein Abbau.

Saccharose und *Maltose* wurden unter dem Einfluß der Drüsenextrakte schon innerhalb der ersten 24 Stunden so stark abgebaut, daß in den Chromatogrammen neben Fruktose und Glukose nur noch Spuren der Ausgangszucker und höhermolekularer Saccharide nachweisbar waren. Langsamer wirkten die Darmextrakte, bei welchen auch nach 10 und 21 Tagen, neben Fruktose und Glukose, in den Chromatogrammen noch größere Mengen der unabgebauten Ausgangszucker und 3—5 neu entstandene Oligosaccharide erschienen (Tab. 1, Abb. 2, 3). Unter den vorliegenden Versuchsbedingungen (Extraktkonzentration, Zuckermenge usw.) bewirkten demnach die Drüsenextrakte schon nach 24 Stunden einen fast völligen Abbau der vorgelegten Saccharose- und Maltosemengen, während

Abb. 8—12. — Papierchromatogramme der Zucker-Hydrolyse unter der Wirkung von Mitteldarm- und Pharynxdrüsenextrakten von gekäfigten Bienen, die mit Zucker- und Zucker-Pollen-Futter ernährt wurden.

V = Vergleichszuckerreihe ; A = Darmextrakte ; B = Drüsenextrakte ; K = Krainerbienen ; N = Nigrabienen ; Z = Zucker-Futter ; P = Zucker-Pollen-Futter.

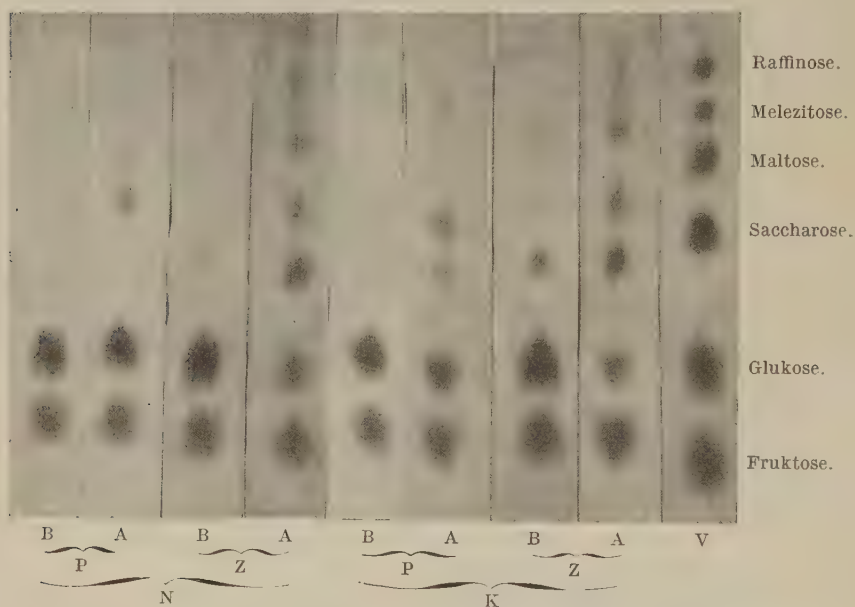


Abb. 8. — *Saccharose*-Abbau, Papierchromatogramme 3 Tage nach Versuchsbeginn.

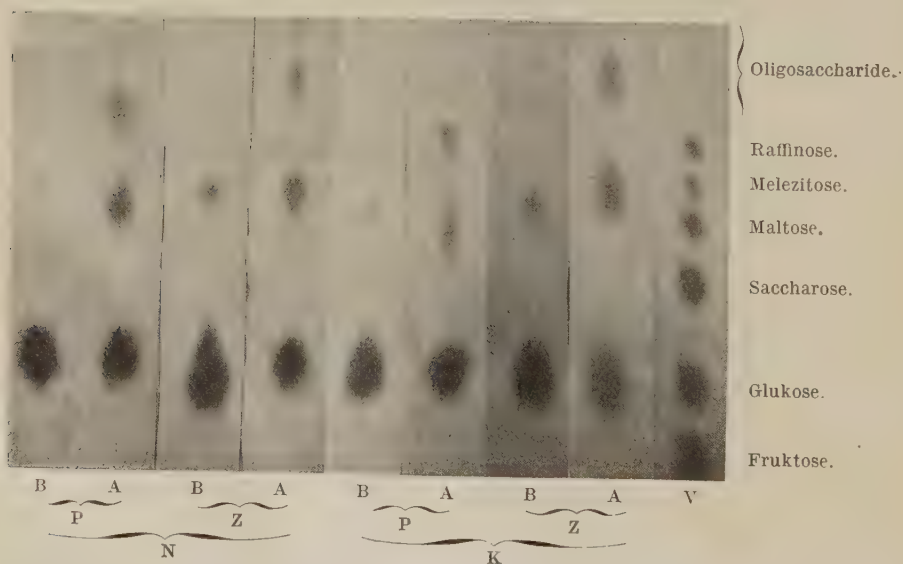


Abb. 9. — *Maltose*-Abbau, Papierchromatogramme 3 Tage nach Versuchsbeginn.

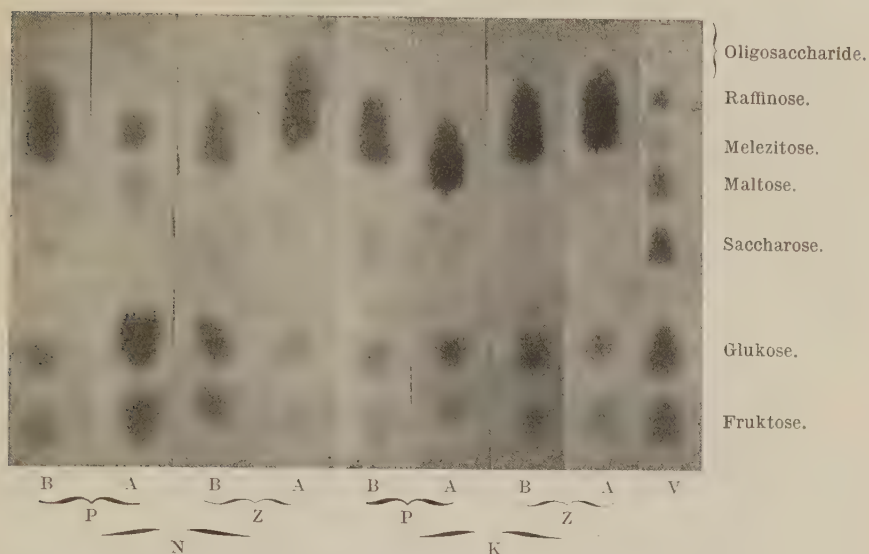


Abb. 10. — Melezitose-Abbau, Papierchromatogramme : Zuckerbienen 21 Tage, Pollenbienen 10 Tage nach Versuchsbeginn.

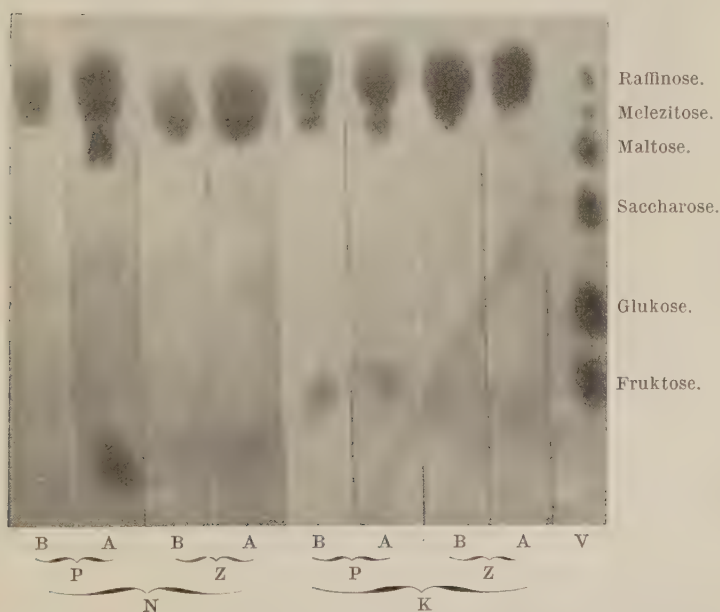


Abb. 11. — Raffinose-Abbau, Papierchromatogramme : Zuckerbienen 10 Tage, Pollenbienen 21 Tage nach Versuchsbeginn.

der Abbauprozess unter dem Einfluß der Darmextrakte nach 10 und 21 Tagen noch in vollem Gange war.

Wesentlich langsamer vollzog sich die Hydrolyse von *Melezitose* und *Raffinose*, bei welchen die ersten Anzeichen einer Spaltung meist erst 3 Tage nach Versuchsbeginn in den Chromatogrammen sichtbar wurden. Auf beide Zuckerarten wirkten die Darmextrakte in der Regel stärker als die Drüsenextrakte, was besonders deutlich in den Serien mit Raffinose zu Tage trat (Tab. 1, Abb. 4, 5, 10, 11). Nur in einzelnen Melezitoseserien war das Verhältnis umgekehrt, d. h. die Drüsenextrakte wirkten stärker (vergl. S. 237).

In keiner der Serien mit Drüsenextrakten unterblieb jedoch die Mele-

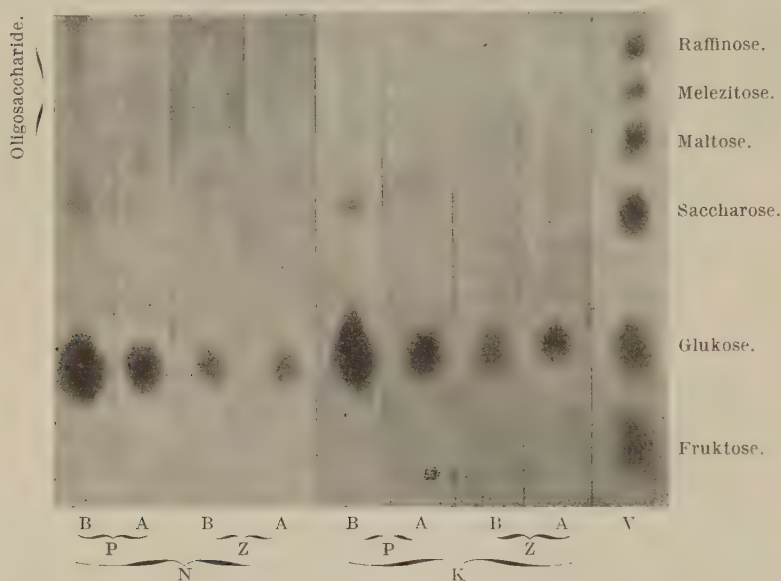


Abb. 12. — *Dextrin*-Abbau, Papierchromatogramme 10 Tage nach Versuchsbeginn.

zitose- und Raffinosespaltung ganz, wenn sie auch manchmal erst nach 10 Tagen begann. Es kann daraus gefolgert werden, daß der Zeitpunkt für einen Nachweis der Hydrolyse für Melezitose und Raffinose später angesetzt werden muß, als für Saccharose und Maltose. Aus diesem Umstand dürften sich die Angaben in der Literatur erklären, wonach Melezitose zwar durch das Darmferment, nicht aber durch das Drüsenferment hydrolysiert wird (GONTARSKI, 1954).

Trotz des verhältnismässig geringen Abbaus der *Trehalose*, waren in den Chromatogrammen deutliche Unterschiede der Wirkung zwischen Drüsen- und Darmextrakten zu erkennen. Die als einziges Spaltprodukt erscheinenden Glukoseflecke waren in den Serien mit Darmextrakten größer und dunkler als in denjenigen mit Drüsenextrakten (Abb. 6). Das geprüfte *Dextrin* wurde von den Drüsen- und von den Darmextrakten gleich schnell und unterschiedslos abgebaut (Abb. 12).

c. EINFLUß DER ERNÄHRUNG UND DES PHYSIOLOGISCHEN ZUSTANDES DER BIENEN AUF DIE WIRKUNG DER EXTRAKTE.

Die Zusammenhänge, welche zwischen der Ernährung und dem mit ihr verbundenen physiologischen Zustand der Bienen, und dem Hydrolysevermögen der Fermente bestehen, lassen sich am besten anhand von Tabelle 1 verfolgen. Sie zeigt vor allem, daß die Extrakte von Bienen aus dem freifliegenden Volk im allgemeinen wirksamer waren als diejenigen aus gekäfigten Tieren. Bei letzteren waren die Extrakte aus den auf Zuckerdiät gehaltenen Bienen weniger wirksam als diejenigen aus „Pollenbienen“, die eine Beimischung von Pollen im Futter erhielten. Dieser Unterschied trat nicht nur bei den Pharynxdrüsenextrakten, sondern auch bei den Darmextrakten auf. Besonders deutlich ist er in den Serien mit Saccharose, Maltose, Raffinose und Dextrin.

In den Serien mit Pharynxdrüsenextrakten aus „Pollenbienen“ war z. B. der *Saccharose*- und *Maltose*abbau nach 10 Tagen praktisch beendet, während in den Parallelserien mit „Zuckerbienen“ zur gleichen Zeit noch beträchtliche Mengen unabgebauter Ausgangszucker vorhanden waren (Abb. 8, 9). In den *Raffinose*-Chromatogrammen erschienen bei „Zuckerbienen“ die ersten Spuren von Abbauprodukten erst nach 21 Tagen; in den dazugehörenden Serien mit „Pollenbienen“ waren sie dagegen schon nach 3 und 10 Tagen sichtbar (Abb. 11). Auch in den *Dextrin*-Chromatogrammen sind zwischen „Pollen-“ und „Zuckerbienen“ deutliche Größenunterschiede der aus der Spaltung entstandenen Glukoseflecke vorhanden (Abb. 12).

Der physiologische Zustand der „Pollenbienen“ (gemessen am Entwicklungsgrad der Pharynxdrüsen) und das Hydrolysevermögen der aus ihnen gewonnenen Extrakte, entsprechen weitgehend denjenigen von Bienen aus dem freifliegenden Volk; bei den „Zuckerbienen“ dagegen blieben die Drüsen völlig unentwickelt und die Wirkung der Extrakte wesentlich schwächer.

Etwas abweichend war das Verhalten der Extrakte aus verschiedenen ernährten, gekäfigten Bienen gegenüber *Melezitose* und *Trehalose*. In diesen Serien blieb die Wirkung der Extrakte aus „Zuckerbienen“ nicht nur hinter derjenigen aus „Pollenbienen“ zurück, sondern es veränderte sich dabei auch das Verhältnis der Wirkung der Drüsen- und Darmfermente. Während bei Bienen aus dem Volk und bei „Pollenbienen“ aus dem Käfig die Darmextrakte eine schnellere Hydrolyse von *Melezitose* und *Trehalose* herbeiführten, wirkten bei den gekäfigten „Zuckerbienen“ die Drüsenextrakte stärker (Tab. 1, Abb. 10). Diese auffällige Beobachtung soll anhand weiterer Versuche nachgeprüft werden.

d. UNTERSCHIEDE DER FERMENTWIRKUNG ZWISCHEN KRAINER- UND NIGRABIENEN.

Die Unterschiede des Hydrolysevermögens zwischen Extrakten aus Bienen der beiden geprüften Rassen blieben in den Versuchen ziemlich

unsicher und schwankend. Gewisse Verschiedenheiten ergaben sich in den Serien mit *Melezitose* und *Raffinose* unter der Einwirkung von Extrakten aus gekäfigten Bienen und in einem der Versuche mit Bienen aus dem Volk. Im allgemeinen führten hier die Extrakte aus Nigrabienen eine schnellere Hydrolyse herbei, als diejenigen aus Krainerbienen (Tab. 1, Abb. 10, 11). Da jedoch diese Unterschiede in der zweiten Melezitoseserie mit Bienen aus dem Volk fehlten und auch in den Serien mit den übrigen Zuckern nicht auftraten, müssen sie mit Vorbehalt beurteilt werden. Auf jeden Fall waren die Unterschiede des Hydrolysierungsvermögens zwischen Nigra- und Krainerextrakten nie so deutlich, wie die von GONTARSKI (1953) für krainer- und portugiesische Bienen beschrieben.

4. DISKUSSION DER ERGEBNISSE

Das Hydrolysierungsvermögen der Bienen- und Honigfermente gegenüber verschiedenen Kohlehydraten ist nach den Ergebnissen der vorliegenden Untersuchung, sowie der Arbeiten von GONTARSKI (1954) und WHITE und MAHER (1953) in Tabelle 2 zusammengefaßt.

TABELLE 2

HYDROLYSIERUNGSVERMÖGEN DER BIENEN- UND HONIGFERMENTE GEGENÜBER VERSCHIEDENEN KOHLEHYDRATEN (nach MAURIZIO, GONTARSKI und WHITE und MAHER).

SUBSTRAT.	DARMFERMENT		DRÜSENFERMENT		HONIGFERMENT White und Maher.
	Gontarski.	Maurizio.	Gontarski.	Maurizio.	
Saccharose	4	3	4	4	4
Maltose	4	3	4	4	4
Trehalose	3	2	0	1	
Lactose		0		0	0
Melezitose	4	3	?	2	3
Melibiose		1		?	0
Cellobiose					0
Raffinose		3		1	1
Dextrin	1	2	1	2	
Stärke (lösl.)	3		3		1
Glycogen	1		1		
Inulin	?		?		

4 = sehr gut; 3 = gut; 2 = mittelgut; 1 = gering; ? = sehr gering; 0 = fehlend.

Im allgemeinen stimmen die Resultate der drei Untersuchungen miteinander überein. Gewisse Verschiedenheiten ergaben sich in der Beurteilung des Hydrolysierungsvermögens der Fermente gegenüber Saccharose, Maltose, Melezitose und Trehalose. Während GONTARSKI einen gleich starken

Abbau von Saccharose und Maltose durch das Darm- und Drüsenferment feststellte, blieb in meinen Versuchen die Wirkung der Darmextrakte deutlich hinter derjenigen der Drüsenextrakte zurück. Daß dieses Verhalten nicht auf Konzentrationsunterschieden der beiden Extrakte beruht, sondern auf Unterschieden der Affinität gegenüber den einzelnen Zuckerarten, beweist der Umstand, daß Saccharose und Maltose von den Drüsenextrakten, Melezitose, Trehalose, Melibiose und Raffinose dagegen von den Darmextrakten stärker angegriffen wurden. Es bestätigt sich dadurch die Annahme GONTARSKI's, wonach in den Pharynxdrüsen und im Mitteldarm der Honigbiene zwei, in ihrer Wirkung verschiedene invertierende Fermente abgesondert werden. Ähnliche Unterschiede der Wirkungsweise hat DUSPIVA (1954 *b*) für Fermente der einzelnen Darmabschnitte von Aphidenarten festgestellt. Das Hydrolyisierungsvermögen der Honiginvertase stimmt weitgehend mit demjenigen des Drüsenfermentes überein. Dies spricht dafür, daß das Honigferment zum größten Teil aus den Absonderungen der Pharynxdrüsen der Bienen stammt.

Nach GONTARSKI wird Melezitose vom Darmferment sehr gut, vom Drüsenferment kaum hydrolysiert; in meinen Versuchen bauten beide Fermente Melezitose ab, wenn auch die Wirkung der Drüsenextrakte schwächer blieb. Diese Beobachtung, die schon von GORBACH anhand von Versuchen mit Extrakten aus ganzen Bienenköpfen angedeutet wurde, findet ihre Bestätigung in den Befunden von WHITE und MAHER, nach welchen auch die Honiginvertase eine ziemlich starke Melezitosespaltung bewirkt.

Die Feststellung, daß das Pharynxdrüsenferment fähig ist, Melezitose zu hydrolysieren, erklärt die von Bienenzüchtern gemachte Beobachtung, wonach schwer schleuderbarer, melezitosehaltiger Honig durch eine Umfütterung im Volk in schleuderbaren übergeführt werden kann; diese Beobachtung wurde von GORBACH experimentell bestätigt. Es dürften sich dabei zwei Vorgänge abspielen, einerseits die während der nochmaligen Verarbeitung durch die Bienen stattfindende Aufspaltung der Melezitose in langsamer kristallisierende Zuckerarten (Fruktose, Glukose), anderseits, falls die Umfütterung zur Trachtzeit vorgenommen wird, eine Mischung des schwer schleuderbaren Honigs mit gleichzeitig eingetragenen, keine Melezitose enthaltenden Rohstoffen.

Ähnlich werden auch Raffinose und Trehalose, die wie Melezitose im Honigtau vorkommen, sowohl vom Darm-, wie vom Drüsen- und Honigferment hydrolysiert (Tab. 2).

Die vorliegende Untersuchung zeigte außerdem, daß direkte Zusammenhänge bestehen zwischen dem physiologischen Zustand der Bienen und im weiteren Sinne ihrer Ernährung und dem Hydrolyisierungsvermögen der von ihnen abgesonderten Fermente. Nur Bienen, welchen pollenhaltige Nahrung zur Verfügung steht, sondern vollwirksame Fermente ab. Ob dabei der Eiweißgehalt oder andere Komponenten des Pollens ausschlaggebend sind, muß in weiteren Versuchen abgeklärt werden. Immerhin dürften neben der Beschaffenheit des Futters noch

andere Faktoren mitbestimmend sein, denn auch Extrakte aus Bienen, welche von Geburt an auf reiner Zuckerdiät gehalten wurden, besitzen die Fähigkeit eine, wenn auch schwächere Zuckerhydrolyse herbeizuführen.

Zusammenfassung.

In der vorliegenden Arbeit wurde mit Hilfe der Papierchromatographie das Hydrolysevermögen der invertierenden Fermente aus Pharynxdrüsen und Mitteldarm der Honigbiene auf folgende Zuckerarten geprüft: Saccharose, Maltose, Trehalose, Lactose, Melezitose, Melibiose, Raffinose, Dextrin. Als Versuchstiere dienten Bienen der Nigra- und Krainer-Rasse, die im freifliegenden Volk und in Käfigen bei unterschiedlichem Futter gehalten wurden.

RESULTATE :

1. Von den 8 geprüften Zuckerarten wurden 6 durch alle Extrakte hydrolysiert, nämlich: stark Saccharose und Maltose, schwächer Trehalose, Melezitose, Raffinose und Dextrin. Bei Melibiose trat ein Abbau erst nach 3 Monaten ein; bei Lactose unterblieb er ganz.

2. Als Produkte der Hydrolyse entstanden bei der Mehrzahl der geprüften Zuckerarten, neben den zu erwartenden einfachen, auch höhermolekulare Saccharide, was beweist, daß die Bienenfermente nicht nur zu einer Spaltung, sondern auch zum Aufbau von Zuckern befähigt sind.

Als Abbauprodukte der Maltose und Saccharose entstanden außer Glukose, resp. Glukose und Fruktose, 3—5 höhermolekulare Saccharide mit niedrigen R_F -Werten. Während des Melezitoseabbaus traten Turanose, Glukose, Fruktose und ein Oligosaccharid auf; der Raffinoseabbau führte zur Bildung von Melibiose, Fruktose, Glukose und eines Oligosaccharids; bei der sehr schwachen Melibiosespaltung erschienen Galaktose, Glukose und ein nicht näher bekanntes Saccharid. Die Hydrolyse von Dextrin und Trehalose ergab eine Anreicherung von Glukose.

3. In allen Versuchen waren Unterschiede im Hydrolysevermögen zwischen den Pharynxdrüsen- und Darmextrakten vorhanden. Saccharose und Maltose wurden von den Drüsenextrakten schneller abgebaut, auf Melezitose, Raffinose, Trehalose und Melibiose wirkten die Darmfermente stärker. Indifferent verhielt sich in dieser Hinsicht das geprüfte Dextrin.

4. Unterschiede der Ernährung und des physiologischen Zustandes der Bienen übten einen gewissen Einfluß auf das Hydrolysevermögen der Extrakte aus. Extrakte aus freifliegenden Bienen und aus gekäfigten Bienen, die Pollen im Futter erhielten, waren wirksamer als solche aus Bienen, die auf Zuckerdiät gehalten wurden.

5. Zwischen Extrakten aus Bienen der Nigra- und Krainerasse waren nur geringe und schwankende Unterschiede festzustellen. Teilweise wirkten die Nigra-Extrakte etwas stärker als die Krainer-Extrakte.

Résumé.

Dans le présent travail, on a étudié à l'aide de la chromatographie sur papier le pouvoir hydrolysant des invertases des glandes pharyngiennes et de l'intestin moyen de l'abeille sur les sucres suivants: saccharose, maltose, tréhalose, lactose, mélezitose, mélibiose, raffinose, dextrine. Le matériel expérimental provenait d'abeilles de races noire et carniolienne prises, d'une part, dans des colonies volant librement et, d'autre part, dans des caquettes où elles recevaient différents types d'alimentation.

RÉSULTATS.

1. Sur les huit sucres examinés, six furent hydrolysés par tous les extraits. Ce sont : le saccharose et le maltose (fortement hydrolysés), le tréhalose, le mélézitose, le raffinose et la dextrine (plus faiblement hydrolysés). Pour le mélébiose, l'hydrolyse n'intervint qu'après trois mois ; le lactose ne fut pas hydrolysé du tout.

2. Pour la plupart des sucres, on trouva comme produits d'hydrolyse, à côté des sucres simples attendus, des saccharides de poids moléculaire plus élevé, ce qui prouve que les invertases des abeilles sont capables, non seulement d'opérer une hydrolyse, mais aussi de provoquer la constitution de sucres.

Comme produits d'hydrolyse du maltose et du saccharose, on trouva, en dehors du glucose ou du glucose et du lévulose, trois à cinq saccharides de poids moléculaire plus élevé, avec une valeur R_F faible. Au cours de l'hydrolyse du mélézitose apparaissent du turanose, du glucose, du fructose et un oligosaccharide ; l'hydrolyse du raffinose conduit à la formation de mélébiose, de lévulose, de glucose et d'un oligosaccharide ; la très faible hydrolyse du mélébiose fait apparaître du galactose, du glucose et un saccharide inconnu. L'hydrolyse de la dextrine et du tréhalose provoque un enrichissement en glucose.

3. Dans tous les essais, on constata une différence entre le pouvoir hydrolysant des extraits de glandes pharyngiennes et des extraits d'intestin. Le saccharose et le maltose sont plus vite hydrolysés par les extraits de glandes ; les extraits d'intestin agissent plus fortement sur le mélézitose, le raffinose, le tréhalose et le mélébiose. A cet égard, la dextrine est indifférente.

4. Les différences dans l'alimentation et l'état physiologique des abeilles exercent une certaine influence sur le pouvoir hydrolysant des extraits. Les extraits d'abeilles volant librement et d'abeilles encagées nourries au pollen furent plus actifs que ceux d'abeilles maintenues à un régime purement sucré.

5. Entre les extraits d'abeilles noires et d'abeilles carnioliennes, on ne constata que des différences variables. Les extraits d'abeilles noires furent partiellement un peu plus actifs que les extraits d'abeilles carnioliennes.

Summary.

In the present study, paper chromatography was used to examine the hydrolysing effect of inverting enzymes from the pharyngeal glands and midgut of the honeybee on the following sugars: sucrose, maltose, trehalose, lactose, melezitose, melibiose, raffinose, dextrin. Experimental material was obtained from bees of the Nigra and Carniolan races, which lived in free-flying colonies or were kept in cages on different diets.

RESULTS:

1. Of the 8 sugars tested, 6 were hydrolysed by all the extracts: sucrose and maltose strongly, trehalose, melezitose, raffinose and dextrin more weakly. With melibiose, hydrolysis set in after three months only; lactose showed no sign of decomposition at all.

2. With most of the sugars tested the products of hydrolysis included the expected simple sugars as well as more complex saccharides. This shows that bee enzymes are capable not only of decomposing, but also of synthesising certain sugars.

The hydrolysis of maltose and sucrose gave not only glucose, and fructose and glucose respectively, but also 3-5 more complex saccharides with low R_F -values. The breakdown products of melezitose consisted of turanose, glucose, fructose and an oligosaccharide; those of raffinose were melibiose, fructose, glucose and an oligosaccharide. Melibiose breakdown, which was very weak, led to the formation of galactose, glucose

and of an undetermined saccharide. Hydrolysis of dextrin and trehalose resulted in an accumulation of glucose.

3. In all the tests, there were differences between the activity of extracts from the pharyngeal glands and from the midgut. Sucrose and maltose were hydrolysed more quickly by the gland extracts, whereas the midgut extracts acted more strongly on melezitose, raffinose and trehalose. Dextrin was equally affected by both kinds of extracts.

4. Differences in the nutrition and physiological condition of the bees had a certain effect on the hydrolysing ability of the extracts. On the whole, extracts from free-flying and from caged, pollen fed bees were more active than those from bees kept on a pure sugar diet.

5. Only small and variable differences could be observed between the extracts from the two races of bees. Extracts from Nigra bees were partly a little more active than those from Carniolan bees.

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BUMBLEBEE ECOLOGY IN RELATION TO THE POLLINATION OF ALFALFA AND RED CLOVER

by

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INTRODUCTION

The major problem of alfalfa and red clover seed production in the United States and Canada is the year to year uncertainty of the seed yields. The wide variations are caused by a complex effect of the environment. Any one of several major factors may seriously limit the growth, flowering, or seed reproduction of the plant. Undoubtedly, pollination is of major importance. Biologists and growers have both recognized for many years that bees are essential for the cross-pollination of most legumes, especially for alfalfa and red clover. Many species of bees are known, but most select flowers other than alfalfa and red clover; or do not exist in numbers adequate to pollinate the extensive acreages which are grown in our present system of grassland agriculture.

It has been only in recent years that honeybees have been managed successfully for the pollination of alfalfa seed crops in the Southwestern United States. In other areas, honeybees have not been managed successfully for the consistent pollination of alfalfa or red clover; although it should be recognized that under some exceptional conditions a measure of pollination may be accomplished by honeybees. Consequently, intensified research on native bees, particularly bumblebees and leaf-cutting bees, would seem fundamental to a practical solution of the pollination problem of alfalfa and red clover in the eastern and northern regions of North America.

FLORAL ECOLOGY.

About a dozen species (2) of bumblebees are found commonly in the areas where alfalfa and red clover are grown in Eastern North America. Space will not be taken to cite literature on their reported floral hosts, or to add records obtained in Wisconsin. It will suffice to say that the data show clearly a polytrophic habit. Many different species of plants in the Rosaceae, Leguminosae, and Compositae are attractive, and records in sixty additional plant families are known. It appears that host records for queens would be more significant than the records for workers from the standpoint of the evolution of floral behavior and the distribution of

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(2) Scientific names of the species are given in table 1.

species. On the other hand, worker records are needed in pollination studies, especially to determine the flower competitors. The evaluation of flower competitors is of practical value, since the elimination of native or cultivated flowers in competition with alfalfa or red clover may force the polytrophic bees onto those crops at times when pollination is desired.

A large bumblebee fauna probably was supported by the native plants of North America before the advent of cultivated crops. A considerable loss or reduction of the native plants followed the clearing of the forest and woodland and plowing of the tall and short grass. There followed a steady increase in the acreage of cultivated legumes, so that today we find alfalfa and red clover extensively grown throughout the deciduous forest and grassland communities. The cultivated legumes may have been important in maintaining the native bumblebee fauna, but no population census is available which would show whether or not the numbers of bumblebees have increased or declined since crops have been cultivated in North America.

Eventually it may be possible to correlate the distribution of bumblebees with that of their preferred native floral hosts. More immediately, a distribution pattern can be discerned on the basis of the records obtained on alfalfa and red clover. More northern species are *Bombus terricola*, *vagans*, and *borealis*; more southern species are *auricomus* and *griseocollis*. *Rufocinctus* is western; *bimaculatus* is eastern. Two species, *fervidus* and *americanorum*, seem to be quite generally distributed, but they are especially abundant on red clover in the middle west. Since the records from red clover and alfalfa are from a wide region, it is believed that climatic factors as well as native floral hosts were important in the past in determining the present-day distribution of the bumblebees.

The floral ecology of Wisconsin bumblebees was discussed by FYE and MEDLER (1954a) from the succession standpoint. The first queens emerging in the spring visit the various species of willow. Next utilized for pollen and nectar are wild and cultivated plums and cherries, and as they fade, dandelion and apple, and subsequently, lilac, *Crataegus* spp., and *Lonicera* spp. become the main food sources. Next is the early attractive bloom of white Dutch clover. Following is the period during which the various clovers (white, Ladino, red, sweet and alsike) and alfalfa become the major source of provisions. The legumes receive some competition from sumac, basswood, thistles, asters and goldenrods, but legumes among themselves are the most serious competitors. In general, the decreasing order of attractiveness found in Wisconsin is white clover, birdsfoot trefoil, alsike clover, sweet clover, red clover, alfalfa. Since the last two are the major seed crop plants, the importance of worker bees of the various species in pollinating those plants has been determined in northern Wisconsin.

B. borealis has a marked preference for red clover, and in the presence of this plant seldom visits other flowers. FRANKLIN (1912) stated that "In no part of its habitat does it appear to be a very common species."

However, in northern Wisconsin this species is very common, exceeded in numbers only by *terricola*.

B. fervidus probably shows the extreme in marked preference. The workers are found on red clover and virtually no other flower, except where there is a marked lack of red clover.

B. vagans visits a variety of blossoms, but it is found on red clover in numbers sufficient to suggest some preference for the plant.

B. griseocollis shows a preference for red clover. It also is an excellent pollinator of alfalfa, but seems to be of minor importance because the workers are too few in number.

B. terricola readily goes to alfalfa and is considered to be the most important bumblebee pollinator of alfalfa in northern Wisconsin.

B. rufocinctus and *ternarius* do not seem to be strongly attracted to red clover or alfalfa. The latter species shows some liking for white Dutch and alsike clovers, but apparently prefers the composites. *B. rufocinctus* is generally a late season bee and reaches a peak population at the time composites are in blossom. It visits goldenrods, asters and sunflowers, in particular.

Fragmentary data have been obtained on the other species. *B. auricomus* and *americanorum* are observed on red clover in the more southern part of Wisconsin.

Certain aspects of floral ecology and bumblebee behavior need investigation. What is the importance of flower color, form and odor in the attraction of the species? Do pollens from different plants have different nutritive value? What inherent behavior patterns are involved in directing bumblebees to flowers, determining the collection of pollen or nectar, and maintaining a fidelity of memory to visited flowers? In connection with the last question, it is interesting to find that CUMBER (1949 *a*) reported on a division of labor between "nurse bees" and "foragers" and that "foragers" could be divided further into individuals visiting flowers with deep nectaries and those visiting flowers with shallow nectaries.

POPULATION ECOLOGY.

In a system of management of bumblebees for pollination, it is essential that suitable numbers of pollen-collecting workers of a major species be available at the time of flowering, and that the field force be maintained over a period of time necessary to pollinate the crop. There are areas where bumblebees may not normally be of practical value in seed production, because of their late appearance, as shown for alfalfa by HOBBS and LILLY (1954). This condition does not seem to prevail generally in the seed areas which have more extended growing seasons.

The species of bumblebees have different colonial cycles, and the species of plants have different sequences of flowering. A coincidental timing of flowering with the emergence of the main brood of workers gives a peak

availability of pollinators. Peak availability does not happen consistently from year to year and may be a critical factor in seed production. Instances have been observed when differences of a week or 10 days in flowering have been the cause of pollination or non-pollination of alfalfa in closely located fields. A knowledge each year of the sequence of appearance of spring queens in conjunction with a prediction of the time of maximum worker production may allow cutting management of a crop so that peak availability is obtained from year to year.

The worker population of a bumblebee colony is the result of an interaction of both biotic and ecologic factors. In the maximum production of workers, importance can be given to the initial vigor of the spring queen, nesting habitat, natural enemies, weather, and food supply. It is known that the colonial cycle, i.e., nest foundation, production of workers, and appearance of the sexes, can be successfully completed, yet the total worker population can fluctuate widely between nests of the same species. PLATH (1934) believed that the keen competition for food was a factor in population differences between nests. He found that in a drouth year starvation caused a general lack of brood in most colonies. Periods of extremely wet weather were detrimental also. Marked differences in abundance and time of worker availability between years were explained on the basis of the weather factor.

It has been convenient to use CUMBER's (1953) division of preworker-emergence factors and post-worker-emergence factors in the following discussion of the development of the worker field force and its maintenance. Initially, a certain loss of bumblebee colonies is caused by the nematode parasite, *Sphaerularia bombi* Duf., which sterilizes the overwintered queen. A recent account of the histopathology has been published by PALM (1948), who found the parasite so common in the vicinity of Lund, Sweden, that it was difficult to obtain healthy bees. In Wisconsin, dissections made in connection with nesting studies of confined bees showed a 10 per cent level of infestation of the parasite. The bees commonly had one or two nematodes in the body cavity and four or five were not infrequent, but six was the largest number found in any one specimen.

With healthy queens, activity in the spring is governed by weather conditions and the availability of food. CUMBER (1949, a) reported that the spring feeding is important for weight increase and ovarian development. If a shortage of nectar exists, a queen may lose vigor and be delayed in the development of ovaries. As the ovarioles swell, a search for nesting sites is begun. The nesting habitat, usually an abandoned rodent's nest, undoubtedly has an influence on the local abundance of a species. FRISON (1923) named four attributes necessary to a bumblebee nest: darkness, dryness, protection, and material to cover the comb. In general, two nesting situations are utilized. One group selects nests on the surface of the ground, or just below the surface. To this group belong *B. fervidus*, *borealis*, *griseocollis*, *americanorum*, *bimaculatus*, *rufo-cinctus*, *auricomus* and *vagans*. A second group, including *terricola*, *affinis*,

impatiens, and *perplexus*, usually nest under the ground. Access to an underground nest is by a tunnel of varying length, which at times may be over 5 feet. The selection of a particular nesting habitat is not invariable, however, and aberrant situations are utilized, such as old birds' nests, hollow tree trunks, and man-made structures.

It might be mentioned here that the surface nesting habit of bumblebees has been adapted successfully for propagating colonies in wooden box domiciles. (FYE and MEDLER, 1954*b*, WILCKE, 1953.) All of the species listed in the first group have been colonized in Wisconsin. However, a satisfactory domicile for the subterranean group has not yet been developed. It has been suggested that underground nests are better protected from the environment, and in this connection it is interesting to note that the most populous bee in North America, *impatiens*, is an underground nester.

A scarcity of nesting habitats and bad weather cause a long period of searching, affect the vigor of the queens, and delay the colonial cycle. Once the nest is established, there are problems of maintaining it against storm damage, the attacks of predators, and lack of food.

The post-worker-emergence factors are in large part associated with maintenance of food supplies and freedom from the attacks of predators and parasites. A major predator of established colonies appears to be the skunk. PLATH (1934) described the methods used by this animal in destroying nests. Major parasites, such as bees belonging to the genus *Psithyrus*, have been discussed by PLATH (1934), FRISON (1926), and CUMBER (1949 *b*).

In the earlier section on floral hosts, the wide polytrophic range of bumblebees was mentioned. A wide availability of hosts may be related to, but is not necessarily responsible for, unlimited nectar or pollen supplies, since bumblebees must compete with honeybees, native bees and other insects for nectar and pollen. Also, nectar and pollen supplies are determined by seasonal growth conditions of the plant. CUMBER (1953) has suggested that an over-abundance of food may reduce the number of workers, for, if the food supplied by the workers is increased in relation to the number of eggs laid by the queen, there may be a change to the production of sexual formas. Ordinarily, an abundance of nectar and pollen would in itself not be expected to be a factor responsible for a lowered worker population. However, it is worth mentioning that thousands of acres of red clover and alfalfa support low populations of bumblebees in much of Wisconsin. It was hypothesized that lack of nesting sites or other unfavorable pre-worker-emergence factors might be a cause, since in northern Wisconsin, where large tracts of native vegetation intersperse the cultivated areas, the legume acreage attracts numerous bumblebees. For example, I have collected as many as 10 workers of *terricola* with a single sweep of a 15" insect net in alfalfa in northern Wisconsin; whereas, in southern Wisconsin it is a rare experience to record bumblebees in alfalfa. Another curious fact is the consistent acceptance of domiciles

in northern Wisconsin, but a very poor occupancy in southern Wisconsin. A critical evaluation of Cumber's food hypothesis may help to explain such phenomena.

Table 1 has been prepared to show the maximum of workers and males and queens which might be produced in colonies of the various species. The records (not necessarily representing the same colony) are taken from the literature, or are unpublished Wisconsin data. The numbers of workers vary between as few as 37 for *griseocollis* and as many as 450 for *impatiens*. Since colonies usually contain fewer bees than the maximums shown, it seems quite evident that environmental factors heavily outweigh biotic factors with regard to the production of the worker population.

TABLE I

MAXIMUM NUMBERS KNOWN FOR WORKERS, MALES AND FEMALES; AND CASTE RATIOS FOR CERTAIN SPECIES OF BUMBLEBEES.

SPECIES OF BOMBUS.	TOTAL workers.	TOTAL MALES and females.	PROVISIONAL caste ratio.
<i>affinis</i> Cress.	175 (Plath, 1934)	46 (Plath, 1934)	4:1
<i>americanorum</i> (Fab.)	108 (Rau, 1941)	332 (Frison, 1930)	1:3
<i>auricomus</i> (Robt.)	55 (Wis. record)	103 (Wis. record)	1:2
<i>bimaculatus</i> Cress.	60 (Plath, 1934)	74 (Frison, 1928)	1:1
<i>borealis</i> Kirby	121 (Wis. record)	203 (Wis. record)	1:2
<i>fervidus</i> (Fab.)	191 (Wis. record)	199 (Wis. record)	1:1
<i>griseocollis</i> DeG.	37 (Wis. record)	45 (Wis. record)	1:1
<i>impatiens</i> Cress.	450 + (Plath, 1934)	500 + (Plath, 1934)	1:1
<i>perplexus</i> Cress.	347 — (Plath, 1934)	50 + (Plath, 1934)	6:1
<i>rufocinctus</i> Cress.	110 (Wis. record)	87 (Wis. record)	4:3
<i>ternarius</i> Say	100 (Plath, 1934)	75 (Plath, 1934)	4:3
<i>terricola</i> Kirby	150 (Plath, 1934)	50 (Plath, 1934)	3:1
<i>vagans</i> F. Smith	112 (Wis. record)	152 (Wis. record)	2:3

The provisional caste ratios shown in table 1 may indicate that inherent differences exist in the biology of species. However, there appears to be a tendency toward a 1:1 caste ratio for most of the species. This may be related to data of CUMBER (1949 *a*) which showed that a change-over of workers to sexes occurred as the brood/worker ratio approached or fell below one. Learning how to manage the biology of bumblebees in order to achieve a more favorable worker ratio would be important to building up the pollinating population.

At the present time, studies of domiciled bumblebees are being conducted in Wisconsin with the objective of learning more about the biologic and ecologic factors influencing populations. Although some measure of control of the environment is accomplished in the wooden box domicile, the difference in populations recorded in the boxes show that a complex problem exists. It is believed that additional research will elucidate the factors and the information subsequently can be used in the propagation of bumblebees for a more controlled pollination of alfalfa and red clover.

Summary.

The ecology of bumblebees has been discussed under two major headings: (1) floral hosts and (2) populations. An understanding of the environmental factors that (1) affect the behavior of bumblebees in visiting flowers and (2) influence the production of a worker field force are basic to the utilisation of bumblebees in a practical way for the increased pollination, or more consistent pollination of alfalfa and red clover seed crops.

Information is presented about the host plants in their seasonal succession, and the attractiveness of various flowers during the period of worker activity. Certain species of bumblebees are shown to differ in their preference of red clover and alfalfa.

The initiation of colonies, the proper development of the brood, and the production of the workers have been related with ecological factors having major influence. Optimum conditions will be required for the culmination of a colony in a maximum force of worker bees at peak availability for pollination.

Worker populations vary widely between species and among colonies of the same species. An elucidation of the reasons for the fluctuations will require additional biological and ecological research.

RÉSUMÉ

L'auteur étudie deux aspects principaux de l'écologie des Bourdons : (1) fleurs visitées et (2) populations. Il est très important de connaître l'ensemble des facteurs d'environnement qui (1) affectent le comportement des Bourdons visitant les fleurs et (2) influencent l'attraction des ouvrières ; cette connaissance peut servir de base à l'utilisation des Bourdons pour accroître la pollinisation de la luzerne et du trèfle rouge.

On donne des détails sur les plantes hôtes au cours du cycle saisonnier et sur l'attractivité des différentes fleurs pendant la période d'activité des ouvrières. Certaines espèces de Bourdons diffèrent par leur préférence entre la luzerne et le trèfle rouge.

Le début des colonies, le développement normal du couvain et la production des ouvrières ont été reliés aux facteurs écologiques principaux. On précise les conditions optimales requises pour que la colonie soit arrivée à son maximum de développement au moment de la pollinisation.

Les populations d'ouvrières varient beaucoup entre les espèces et entre les colonies d'une même espèce. L'auteur espère élucider ces différences dans des recherches ultérieures.

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TAXONOMIC STATUS OF *FORMICA SUBNITENS*
CREIGHTON AND *F. INTEGROIDES* EMERY,
WITH A DESCRIPTION OF THE SEXUALS OF
F. SUBNITENS (HYMENOPTERA: FORMICIDÆ) (1)

by

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During the summers of 1954 and 1955 Mr. G. L. Ayre, now of the Entomology Laboratory, Belleville, Ontario, studied the species *Formica subnitens* Creighton and *F. integroides* Emery in the field at Westbank, British Columbia. He obtained several series from nests and forwarded them to the author for identification. According to Creighton (1940, 1950), the forms were determined as *F. integroides* Emery and *F. integroides subnitens* Creighton. The writer was impressed with the consistent difference in integumental sculpture of the two ants and suggested to Mr. Ayre that close field observations of habits might reveal important ecological data that would aid in determining whether they were species or subspecies.

In October, 1955, Mr. Ayre forwarded additional nest material of the two forms from the same area with ecological notes. Association of these data with the above morphological difference and examination of the sexual of both kinds showed that these two entities are specifically distinct.

Cole (1955), on very meagre distributional evidence, elevated *F. integroides subnitens* to a specific level. The morphological, ecological and distributional data in the following table confirm Cole's assumption.

SEXUALS OF *F. SUBNITENS*

The following descriptions and measurements were made from specimens killed in 70 per cent alcohol; the females include replete and non replete forms. The measurements were taken immediately on extraction from the alcohol.

(1) Contribution No. 3480, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.



Fig. 1 (left). — Typical nest and nest site of *F. subnitens*.

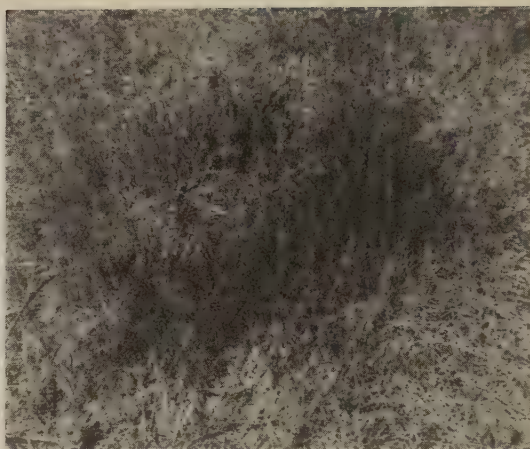


Fig. 2 (right). — Close-up of typical nest of *F. subnitens*.

F. subnitens.

F. integroides.

MORPHOLOGY.

Form.	Body Length,	Mesonotal Width,	Form.	Body Length,	Mesonotal Width,
—	mm.	mm.	—	mm.	mm.
♂	7.5 — 9.5	1.5 — 1.8	♂	9.0 — 11.5	1.8 — 2.0
♀	6.6 — 9.5	1.0 — 1.3	♀	9.0 — 11.5	1.7 — 2.0
♀	4.7 — 8.2	0.37 — 0.65	♀	5.0 — 9.0	0.44 — 0.88

(Based on 33 ♀♀ from 3 nest series, 26 ♂♂ from 3 nest series and 45 ♀♀ from 3 nest series.)

(Based on 19 ♀♀ from 3 nest series, 31 ♂♂ from 4 nest series and 45 ♀♀ from 3 nest series.)



Fig. 3. — Typical nest and nest site of *F. integroides*.

Integumental sculpture.

♂	strongly shagreened and opaque.	♂	minutely punctate and opaque.
♀	finely shagreened and very shiny.	♀	minutely punctate and opaque.
+	finely shagreened and very shiny.	+	minutely punctate and opaque.

ECOLOGY.

Nest site and structure.

Open, dry grasslands of Transition zone.	Open woodlands of Transition zone.
Dense vegetation encircling nest.	No vegetation encircling nest.
Shape — domelike.	Shape — domelike.
Diameter — 16 in. (approx.)	Diameter — 4 ft. (approx.)
Height — 6 in. — 8 in.	Height — 2 1/2 ft. — 4 1/2 ft.

Nuptial flight.

Middle to end of June.	Latter part of May to early June.
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DISTRIBUTION.

<i>United States.</i>	<i>Canada.</i>	<i>United States.</i>	<i>Canada.</i>
New Mexico.	British Columbia.	California.	British Columbia.
Oregon.		Oregon.	
		Washington.	

FEMALE (fig. 4,A).

Body length.—(From the front margin of the head to the hind margin of the abdomen, the body being in the same position as in figure 4,A) 6.6—9.5 mm.

Mesonotal width.—(Immediately in front of the tegulae) 1.0—1.3 mm.

Head.—Occipital border straight or slightly convex; occiput and front with one to three long erect hairs; anterior border of the clypeus with a row of erect hairs; disk of the clypeus with zero to four erect hairs, gula with one to three erect hairs; compound eyes covered with short, fine, golden, erect hairs; pilosity consisting of widely spaced, short, inconspicuous, golden hairs; integument minutely shagreened to smooth and very shiny.

Thorax.—The 10 to 12 erect hairs of the dorsum much shorter and more obscure than those of the head; tegumental sculpture slightly stronger than that of the head and not as shiny; pilosity longer and more abundant than that on the head.

Petiole.—Dorsal margin convex, sometimes impressed in its middle portion.

Abdomen.—Erect hairs of all but the apical two tergites widely spaced, about as long as those of the head and mostly confined to the apical margins; erect hairs of the apical two tergites and all the sternites approximately a third longer; pilosity of the tergites short and fine, barely obscuring the smooth, shining integument.

Color.—Apparently relatively stable; ground color of head, thorax, and petiole yellowish-red; fuscous markings on mandibles, anterior margin

of clypeus, front, occiput, posterior margin of prothorax, entire meso- and meta-nota, tegulae, and dorsal edge of the petiole; legs almost entirely brownish; abdomen brown.

MALE (fig. 4,B).

Body length.—7.5—9.5 mm.

Mesonotal width.—1.5—1.8 mm.

Head.—Antennal scape slightly longer than the first four funicular segments; dorsal half of head quadrate, anterior half about two thirds

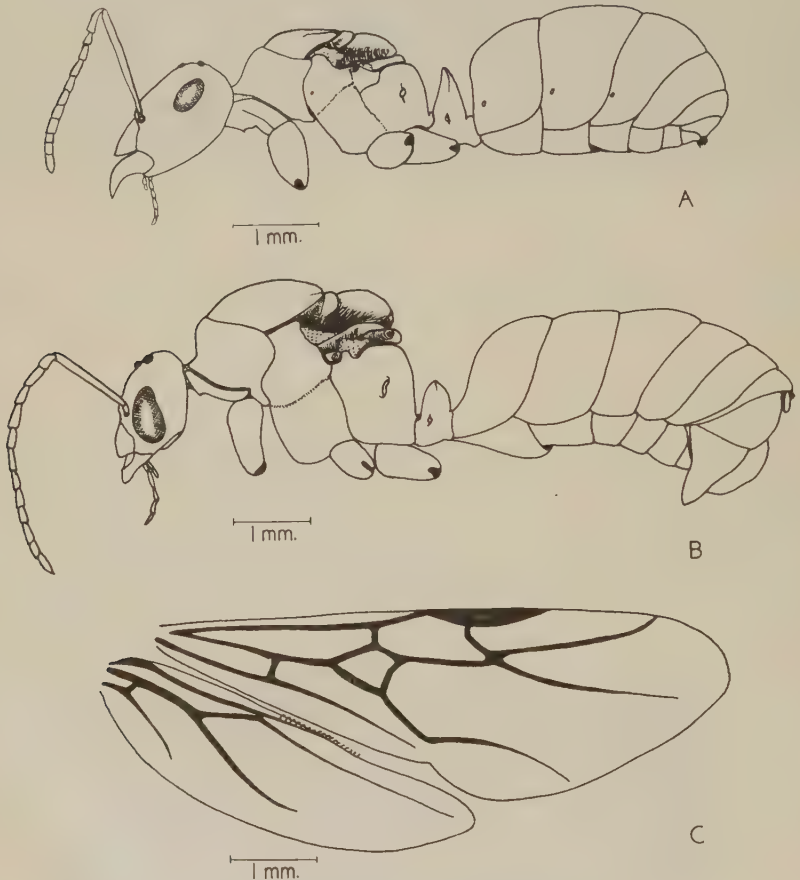


Fig. 4. — Outline drawings of *F. subnitens*.
A, female; B, male; C, male fore and hind wings.

as wide as posterior half and tapered anteriorly; decumbent to subdecumbent, long, greyish, coarse, and numerous erect hairs on the elevated occiput, occipital angles, gula, and anterior half of the clypeus; erect hairs of the bulbous compound eyes short, greyish, and numerous; mandible triangular, with a single apical tooth; integumental sculpture of the head strongly

shagreened and opaque, except for the smooth, shiny front, gular disk, and mandibles; pilosity sparse and greyish, somewhat clustered at the anterior edge of the gena near the base of the mandible.

Thorax.—Erect hairs abundant, long, and numerous on entire dorsum and pleura; integumental sculpture strongly shagreened and opaque; pilosity long and greyish, partially obscuring sculpture of mesonotum.

Petiole.—Dorsal margin straight to slightly concave, bearing 4—5 long erect hairs.

Abdomen.—All but the first and last tergites devoid of erect hairs; short greyish pilosity partially obscuring the strongly shagreened, opaque, integument.

Color.—Head, thorax, petiole, and legs black; abdomen brown and the protruding genital structure yellowish.

Wings (fig. 4,C).—Veins light fuscous and the stigma brown.

Summary.

Field and laboratory data on *Formica subnitens* Creighton and *F. integroides* Emery confirm Cole's assumption that these entities are species. The female and male of *F. subnitens* are described.

Acknowledgments.

The writer is indebted to Mr. G. L. Ayre, Entomology Laboratory, Belleville, Ontario, for the material and ecological notes he supplied; without his co-operation the ecological data would not have been available. Thanks are due Dr. W. S. Creighton, College of the City of New York, for sending a paratype of *F. subnitens* for comparison and for confirming the writer's identification of the material used in this study. Thanks are also due Dr. A. G. Cole, University of Tennessee, for supplying the writer with his publications on *F. subnitens*.

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A COMPARISON OF SPECIES AND GENERA IN THE ANT SUBFAMILY DORYLINÆ WITH RESPECT TO FUNCTIONAL PATTERN (1) (2)

by

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(The American Museum of Natural History.)

OUTLINE

The Eciton Functional Pattern.

Eciton hamatum as typical of the genus.

Two prominent Eciton species compared.

The Dorylus Functional Cycle.

Species typifying the African subgenus *Anomma*.

Comparison of *A. wilverthi* and *nigricans*.

Comparison of *Anomma* and *Eciton*.

General similarities and differences.

Environmental adaptations in *Anomma* and *Eciton*.

Reproductive function and cyclic behavior in *Anomma* and *Eciton*.

Basic control of functional rhythms in *Anomma* and *Eciton*.

Summary Discussion.

Conclusions.

Résumé.

INTRODUCTION

The dorylines are a distinctive ant subfamily characterized by relatively large colonies maintained through predatory activities supporting a carnivorous diet and a nomadic way of life. In this paper we shall be interested in comparing the nomadic pattern of some of the members of this group, in order to find what may be common to all members of the subfamily and what may be specific to certain sections of it.

The doryline ants are mainly indigenous to the tropics, in which the main course of their evolution evidently occurred, perhaps in the late Jurassic and early Tertiary periods (30). Best known at the present time in their behavior and biology are the Ecitons or army ants of the New World (7, 8, 14, 21, 22) and the Dorylus or driver ants of Africa (3, 11, 12, 26). These members of the continentally separated tribes Ecitonini and Dorylini present certain broad similarities as well as some striking differences (22), both of great interest in view of the fact that their common evolution may have ended when derivatives of a pre-doryline ancestor separated (2, 4).

In this paper the general *Eciton* and *Dorylus* will be compared functionally as far as

(1) This study is dedicated to Prof. Dr. Karl von Frisch on the occasion of his 70th birthday.

(2) Study of preserved material collected in field investigation, an essential part of this project, has been aided by a grant from the National Science Foundation; earlier phases of the research were supported through a contract between the Office of Naval Research, Biological Branch, and the American Museum of Natural History.

possible in a way which may suggest how far common characters may have persisted, and to what extent disparate characters may have appeared, in the subsequent evolution of the continentally separated lines in this subfamily. This problem will also be considered with respect to certain sympatric groups within the genera.

Attention is called to the fact that in this comparison we shall be dealing with those members of two continentally separate doryline tribes which happen to be best known at the present time. This will be an advantage at least in that the comparison will involve one group (genus *Eciton*) whose members evidently have become specialized functionally in ways very divergent from the pattern of the hypothetical pre-doryline ancestor, with another (genus *Dorylus*) evidently less specialized in comparison with *Eciton*.

THE ECITON FUNCTIONAL PATTERN

Eciton hamatum as typical of the genus.—Recently the group formerly identified as the subgenus *Eciton s. str.* has been designated a distinct genus (*Eciton*) by BORGMEIER (1), and separated as such from three other newly distinguished genera of American dorylines, one (*Nomamyrmex*) newly named and two others (*Labidus* and *Neivamyrmex*) raised from subgeneric rank. Carried out on systematic and morphological grounds, this development also has great value from the standpoint of behavioral and ecological characteristics, that is, with respect to *functional* considerations. In habitat and adaptive behavior the species of *Eciton* are all dominantly epigaeic, adapted to nesting and to activities mainly on or above the floor of the tropical forest. In contrast, species in the three other genera are more or less dominantly hypogaeic or subterranean in habitat and adaptive pattern (22).

The two *Eciton* species to be compared here are the most epigaeic in their genus, and therefore best suited to bring out the evolutionary trend which seems to distinguish their group from other genera in the tribe Ecitonini and from genera in the Dorylini.

To establish the characteristics of the *Eciton* functional pattern in broad outline, the case of *Eciton hamatum* will serve. A schema of the principal adaptive characteristics of this species is offered in Figure 1. In considering the *Eciton* pattern, we may at the same time review the outlines of a theory which I advanced in 1938 (14) to explain this pattern and which may be offered as the logical framework for studying adaptive functions characteristic of the doryline ants in general.

The four principal aspects of the *Eciton* pattern are: 1) the functional, cycle, 2) the brood cycle, 3) nesting condition and 4) raiding pattern. These characteristics of the *Eciton* adaptive system are represented in Figure 1 in terms of their concurrent variations over a period of time in a colony normally active in the natural situation. The described characteristics of the *nomadic* condition and of the *statory* condition occur in two distinctive patterns typifying the two very different functional phases of the *Eciton* cycle (20). These two conditions are so clearly differentiated that it was possible to describe them reliably after an initial field investigation of only a few weeks (13).

The principal features of the two functional phases of *Eciton* will be briefly reviewed here in terms of conditions for *E. hamatum*, together with the theory offered to account for the repetitive occurrence of these phases through the life of a colony.

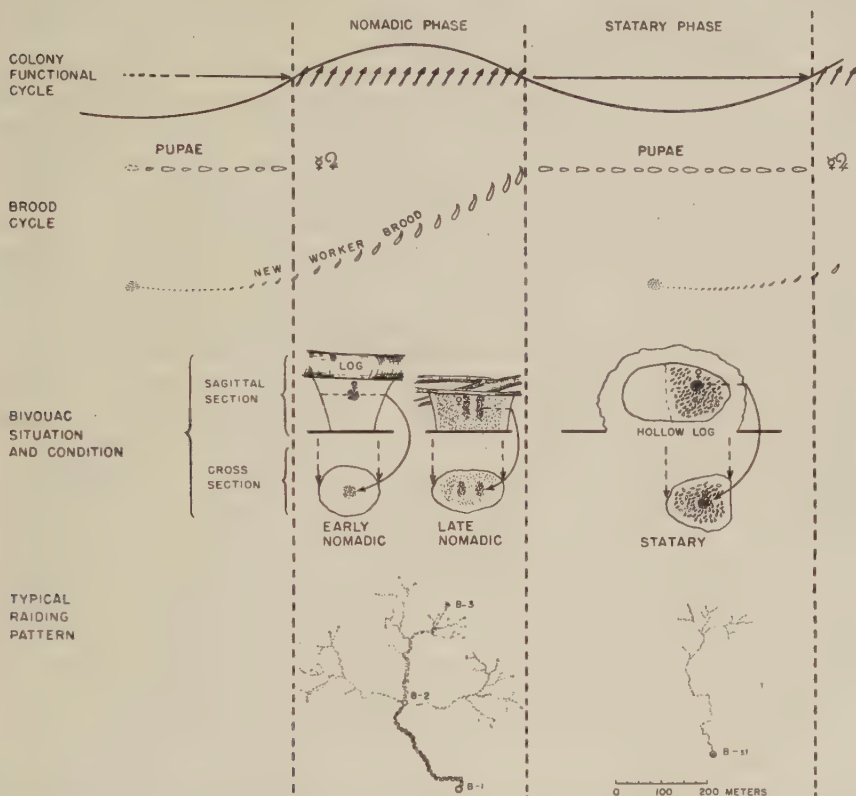


Fig. 1. Schema representing concurrent events in the nomadic and statary phases of the *Eciton* functional cycle, based on *E. hamatum*.

Colony functional cycle. — Crest of sine wave, *nomadic phase*: arrows represent large daily raids, ending in nightly emigrations. Trough of sine wave, *statary phase*: line represents reduced raiding, absence of emigration.

Brood cycle. — One complete brood series is represented, from left, eggs, larvæ, and enclosed prepupal and pupal stages, to newly emerged callow workers at right.

Bivouac. — At left, exposed bivouac cluster of the nomadic phase, suggesting principal changes in brood distribution; at right, sheltered bivouac of the statary phase, suggesting new brood as egg mass centered below queen, advanced brood as enclosed pupæ.

Raiding pattern. — Left, three-system raid of the nomadic phase, developed from the bivouac at B-2; previous night's emigration line, B-1 to B-2; emigration line after end of current raid, B-2 to B-3. Right, single-system raid of the statary phase, from the fixed bivouac site B-st.

The *nomadic phase* is the maximally active time of the functional period. In this phase a large raid builds up daily from dawn, in the case of *E. hamatum* approximating the three-system type sketched in Figure 1. After dusk, the colony emigrates along one of the principal trails established

in the raiding. At the beginning of this phase, an all-worker brood (exceptionally, a sexual brood,—23) emerges from cocoons and is incorporated into the population. At this time a further all-worker brood is present, in the early stages of larval development. The nomadic condition of large daily raids and regular nightly emigrations continues until this brood has reached larval maturity. Each new bivouac, or temporary nest, is established usually at 200 meters or more from the preceding one, forming as a largely exposed cluster of workers hooked into an outer wall with a looser internal structure enclosing the queen and brood (24). In this phase the queen lays no eggs, and her gaster remains contracted, minimal in size. At first the young brood is massed in a single bolus at the center of the bivouac cluster. As the larvae grow, this brood occupies an increasing space in the bivouac, with the larger members of the polymorphic series at the periphery, the smaller members more central in relation to their size. When the members of this brood attain larval maturity (the largest members or potential workers major first, the smallest members a few days later), and most of them have completed the first stages of spinning and enclosure within cocoons, the nomadic phase ends.

There follows a *statory phase* which in this species commonly lasts 20 days. The word "statory" a reclaimed English word meaning "standing in place", best designates this interval, in which the colony remains in the same nest and operates at a distinctly reduced metabolic level. As Figure 1 indicates, this phase is characterized by an absence of emigrations and by small daily raids. The bivouac cluster is established in an ecologically sheltered place, as within a hollow tree or log, and the colony is much less excitable and active than in the nomadic phase. But meanwhile, a significant reproductive event occurs. Starting in the last days of the preceding nomadic phase the queen has been entering the physiogastric condition, completing the maturation of a full brood of oöcytes; now, during the second week of the statory phase she becomes fully gravid and delivers a new brood of eggs. During this time the advanced cocoon-enclosed brood has been pupating, and the current statory phase ends precisely at the time when this brood is mature and emerges from cocoons as callow workers.

Thus two distinctive patterns of events recur alternately in Eciton colony function, the principal conditions of each pattern always occurring together. Nomadic and statory phases alternate as described in regular functional periods throughout each year and throughout the life of each colony, —that is, during a few years, the life span of the colony queen. The one normal variation of any importance is a shortening of the nomadic phase by a few days when a sexual brood passes through its larval stage (23).

A causal nexus is involved in each of these patterns of concurrent events, clearly indicated by evidence from field and laboratory studies. The gist of the matter is that each of the two functional phases and the nomadic—statory cycle itself are accounted for by the high excitatory effect exerted upon the worker population by active broods. The nomadic

phase occurs when first the properties of newly-emerged callows and then of active larvae serve to raise the level of social stimulation and lower the excitatory threshold of workers to the point at which the colony is capable of forming large and vigorous daily raids. Each raid of this maximal type leads into a nighttime emigration by an inevitable series of steps (13, 14), and the energy output of the colony then remains near its peak. Nomadism is maintained thereby, as emigration is a behavior pattern regularly succeeding the maximal diurnal raid, an inevitable sequel of the behavioral situation arising through such a raid (14, 17).

In this phenomenon, the active brood may be considered an *excitement center* in the colony, delivering from its central position a continuous massive stimulative effect exerted through innumerable tactual and olfactory encounters between brood-and-workers and workers-and-workers. A high rate of stimulus-permutation is thereby maintained through the constant, intimate association of workers and brood, spreading through the colony in continuous waves of propagated excitement. There are indications that the communication of such stimulative effects varies in its maximal level according to colony size (*i.e.*, worker population), and that the behavioral outcome may thereby differ qualitatively. This consideration holds for the comparison of colonies both within a species and between different species and genera.

On this basis, the emergence of a large new brood of mature pupae as active, voracious callow workers introduces a *callos-stimulative effect* which accounts for the initiation of a nomadic phase (14, 17). But within a few days the force of this excitatory effect wanes as the callows darken in exoskeletal pigmentation and drop off in their excitement to a level approximating that of adult workers. Why, then, does nomadism continue regularly beyond this time, in *Eciton* species? It is because a further brood-excitatory factor enters the field, well synchronized with the waning callow-excitatory factor.

In the first days of the nomadic phase, the stimulative effect of the larval brood always present at this time is low. However, by the fifth day the excitatory effect of this brood has increased to a level at which it replaces the ebbing callow factor as the principal energizer of nomadism. This synchronization is attributable partly to the fact that the two broods are actually competing trophically, with the young larval brood reduced in food supply and held back in development until the callows have mainly completed their post-eclosion maturation. As the larval brood grows, colony excitement increases until it approaches the high level typical of the first two nomadic days. Thus in *E. hamatum*, usually for 17 days and less frequently for 16 days, the nomadic condition is continuous. When the larvae are mature and enclosed, their stimulative effect upon the colony falls to a much lower level, and the stately condition ensues (22).

The stately phase is not a time of constant minimal activity, with excitatory processes at a low level dependent upon workers (and queen) only,

and the brood excluded as a factor. Actually, a brood-excitation effect continues although much reduced, varying according to brood condition. This is indicated first of all by the fact that during the first few days as well as the last few days of the phase, daily raids are more regular and vigorous on the whole than in the remaining days. The reason is that as the statary phase begins, the population exhibits a level of excitement which falls off when spinning activities have been completed in the enclosed brood. Movement and odors of the spinning larvae seem responsible. And comparably in the final days of the statary phase (which usually lasts 20 days in *E. hamatum*) a noticeable growing excitation of the workers occurs, attributable to stimuli arising through pupal maturation in the brood. Not only are the evident effects of antennal, tarsal and body-bending reflexes to be considered as causes, but no doubt olfactory effects as well. Also, midway in the statary phase, colony excitation rises somewhat within the few days when egg-laying is at its peak. Although these brood effects account for limited increases in the frequency and vigor of raiding, normally they are never sufficiently strong to bring the colony to the threshold of emigration.

These are some of the facts indicating that the general level of colony excitation in Eciton depends upon specific stimulative effects emanating from the brood. The behavioral effect of the excitation communicated through the worker population is dependent largely upon the capacity of the brood to deliver a total stimulative impact of given intensity in a given time. This is the main and essential cause accounting for nomadism. The teleological conceptions that scarcity of food in an area causes emigration, or that the brood needs food and therefore excites the colony are obscure and actually misleading (14, 22).

It is now apparent that, since the phasic changes of the Eciton cycle depend upon brood condition, and since the queen delivers the large unitary broods at regular intervals, whatever determines the queen's reproductive rhythm must serve as principal controller of the colony functional cycle. We must go slowly here, for the detailed control of reproductive rhythms is not known very well for any social insect. Although the question of what stimulates the Eciton queen to become physogastric and deliver a new brood is no doubt very complex in detail, I have had occasion to consider the problem in a preliminary manner as evidence has grown slowly during the past ten years (14, 16, 22). The available facts have led me to discard not only the concept of a strictly endogenous control in the queen, but also that of a physical rhythm in the environment independent of the colony situation, as timing mechanisms controlling the rhythm. Actually the Eciton rhythm (two phases in a period of 35-37 days in *E. hamatum*) does not coincide with any periodic physical change such as lunar cycles, and furthermore, numerous colonies studied concurrently are found to pass through their functional periods not synchronously, but in all possible phase relations with one another. Rather, physogastry evidently arises as a response of the queen to a stimulative and trophic

situation which exists in the colony at the time a larval brood is nearing maturity, and continues to its completion in egg-laying as the product of colony conditions of equivalent effect. Evidently, the queen's ovulative condition varies in time primarily according to the action of the colony situation upon her metabolism and behavior.

For what follows, it is necessary to examine further the relationship of the Eciton queen to her colony situation. During the principal part of the nomadic phase, as the larval brood grows, the queen remains fully contracted. HAGAN's histological studies (9) show that her reproductive processes, involving two overlapping generations of immature oöcytes in her ovarioles, progress at a very slow rate. But a few days before the nomadic phase ends, the queen's fat bodies recrudescce, and not only does the advanced oöcyte generation begin a spurt to maturity but there is also a limited acceleration of the younger oöcyte generation. It is significant that these reproductive advances occur at the time when the maturing larval brood changes abruptly in its relation to the colony, consuming less and less food while at the same time increasing to a maximum in its excitation of the worker population. Histological studies (10, 25) show that at this time the larval salivary tissue atrophies progressively, as the spinning-gland tissue develops. The colony stimulative and trophic situation then changes complexly, and the possibility of chemical substances, produced thereby in brood or colony and influencing changes in the queen, cannot be excluded. In any case, the fact is that the stimulative responses of workers to the queen (for example, as observed in the nightly emigration) intensify greatly at this time, and that in the bivouac workers heap food in increasing quantities around the queen. However, progress of the queen toward physogastry is probably much more than a direct reaction to abundant food. Food surpluses may exist at other times in the cycle without having this effect. It is more likely that excitation of the queen to voracious feeding is effected through the licking and other social-stimulative responses of workers to her, at this time when the colony is highly aroused through brood changes. The onset of physogastry and laying in the Eciton queen evidently results from both stimulative and trophic changes introduced into the colony situation as each further larval brood nears maturity.

Available evidence indicates that the functional pattern as outlined for *E. hamatum* typifies that of other species of *Eciton* studied in this program. But this is only an outline. A better understanding of what is essential to the Eciton adaptive system may be obtained through a consideration of similarities and differences among certain species in the genus.

Two prominent Eciton species compared. In Table I are listed the principal characteristics of two of the most epigaeic species in this genus. *E. hamatum* and *E. burchelli*, both widely distributed in the American tropics from about 20° N. to 20° S. A comparison of these species should

TABLE I

Species comparison in Eciton.

	<i>E. hamatum.</i>	<i>E. burchelli.</i>
Functional cycle.	Nomadic phase, 16-18 days (Mode, 17). Statory phase, 18-21 days (Mode, 20).	Nomadic phase, 11-16 days (Mode, 13). Statory phase, 19-22 days (Mode, 21).
Raiding pattern.	Branching-column pattern, small terminal groups.	Swarm pattern: large advance group, basal fan, consolida- tion column.
	Foraging mainly on ground.	Swarms on ground; frequently in vegetation, high in trees.
Bivouac.	Exposed nomadic clusters, shel- tered statory clusters; more often lower, underground.	Exposed nomadic clusters, shel- tered statory clusters; more often higher above ground, in trees.
Brood.	Worker brood, 60,000 + Sexual brood (at maturity), ca. 1,500 males, 6 queens.	Worker brood, 120,000 + Sexual brood (at maturity), ca. 3,000 males, 6 queens.
Colony population.	150,000-250,000.	300,000-1,500,000.
Range of worker sizes.	Body length: 3.2-12.8 mm.	Body length: 3.7-13.7 mm.
Worker behavioral repertoire.	Lower excitability range, retreat at lower stimulus intensities; soft bodied prey.	Wider, higher range of excita- bility, retreat at higher stimulus intensities; hard- bodied, larger prey also.
Brood: relation to colony.	Callow-excitatory effect initiates nomadic phase; larval-excita- tory effect continues phase to end. Pupal brood generally all emerged before 1st nomadic emigration completed.	Callow-excitatory effect initiates nomadic phase; larval-excita- tory effect continues phase to end. Pupal brood seldom more than three-fourths emerged before 1st nomadic emigration com- pleted.
—estimated developmental stages.	.egg to larva, 10 days .larval stage, 16 days. .enclosure to pupal maturity, 20 days.	... 10 days. ... 13 — ... 21 —
—estimated brood time- range.	.at laying, 7 days. .at spinning, 3-4 days. .at eclosion, 2-3 days.	... 10 — ... 7 — ... 5-6 —
Queen (Gaster variations in cycle).	Contracted gaster, 9.4 mm.; physogastric, ca. 19.5 mm.	Contracted gaster, 10.1 mm.; physogastric, ca. 21.5 mm.
Total number of ovarioles.	est. 1,800.	2,600 (Hagan—9).
Duration of egg- laying.	ca. 7 days (peak, 2-3 days).	ca. 10-12 days (peak, 3-4 days).
Eggs in each brood.	60,000 +	120,000 +

greatly assist a study of adaptive function in this genus and facilitate its comparison with that in other dorylines.

Differences between these two species may be characterized by saying that *burchelli* has a greater range and greater variability in many important aspects of its behavior and biology than has *hamatum*. For example, the corresponding types of individuals are larger and stronger in *burchelli*,—both queen, males, and the workers through the polymorphic range. In *burchelli* the colony populations are larger, generally more than twice as large, and their size range is much greater than in *hamatum*. In the production of single broods the *burchelli* queen has a capacity perhaps twice that of *hamatum*, and requires a longer time to lay these eggs than does the *hamatum* queen. A striking difference in colony behavior is that *burchelli* more commonly invades the trees and higher vegetation, mounting higher and in far greater numbers than does *hamatum*. This is one factor contributing to the more frequent formation of arboreal bivouacs by *burchelli*, whose colonies range much higher from the ground than those of *hamatum*.

These species both have well-defined nomadic-statory cycles, based upon common properties as concerns the stimulative relationships of workers and broods, of queen to colony, and the like. In contrast to a minor difference in the duration of the statory phase, with that of *hamatum* tending to be slightly shorter, *burchelli* has a considerably shorter nomadic phase, more variable in duration than that of *hamatum* (20). The latter difference is clearly attributable to factors influencing larval development. Prominent among these is the higher central temperature characteristic of the larger *burchelli* bivouac in the nomadic phase (24). No doubt the time relations of phases in the cyclic pattern depend upon still other characteristics of the community and its microclimate in the two species.

Another factor contributing to the described species differences in phase durations may concern differences in the ratios of brood-stimulative effects to brood and population magnitudes in the colonies. It is interesting to note that both the beginning and the end of the nomadic phase are less predictable in *burchelli* than in *hamatum*, in their specific time relations to brood condition. In *burchelli* the nomadic phase commonly begins with one-third or more of the mature pupal brood (the smallest sizes) still in cocoons, and complete eclosion of this brood is not completed until three or four days after the phase has begun. In *hamatum*, on the other hand, eclosion of the mature brood generally is completed before the first emigration of the phase has ended, so that few if any cocoons are carried along unopened. A comparable difference is observed at larval maturation and the cessation of nomadism. When in *hamatum* a colony settles into its statory bivouac, spinning generally is well under way throughout the brood, whereas the initiation of spinning in the smaller castes typically is more delayed in *burchelli*, and emigration occurs before its delayed completion. A relation of such differences to population magnitude is indicated by the fact that variability is greatest and the delays longest in the

largest *burchelli* colonies; also, when abnormal cases are found in these respects in *hamatum*, colonies of maximal size are involved. In doryline colonies with larger brood and adult populations, communicative permutation of brood-stimulative excitation adequate to arouse emigration may be achieved through the colony without the entire brood being involved.

The described species difference also rests upon a greater time range in developmental rates through the polymorphic brood in *burchelli* than in *hamatum*. In *burchelli* the queen requires a longer time to produce her larger brood of eggs, contributing to a greater time differential than in *hamatum* between the largest individuals (potential workers major) and the smallest individuals (potential workers minima) in their arrival at corresponding stages of development. The former, developing from eggs laid first in the series, clearly have a large time advantage over the latter. In both species, the developmental rate is faster in individuals of smaller size; nevertheless, in *burchelli*, this differential does not reduce the initial time gap as much as in *hamatum* (10, 25). Also, the processes of brood development seem to be more variable in *burchelli* (Table I). Yet in both species the development differential through the brood is sufficient to admit a much stronger stimulative impact from the brood both at larval and at pupal maturity than would be the case were growth rates more uniform. This characteristic is significant for comparisons of colony function in *Eciton* with that in other doryline genera.

One major consequence of the difference between the developmental patterns of these *Eciton* species seems to be a relatively greater overlap in *burchelli* of the callow- and the larval-stimulative factors supporting nomadism in the early part of the phase. In *burchelli* the callow-stimulative factor declines and the larval-stimulative factor rises at slower rates, so that a summative action of these factors evidently is important for a longer time than in *hamatum*. The interval within which summation is critical seems to run from about the third to about the fifth nomadic day in *hamatum*, but to about the seventh nomadic day in *burchelli*. This is a crucial time, when exceptional weakening of either brood-stimulative factor can reduce or stop nomadism (20). The greater overlap in *burchelli* may be an essential adaptive device operating against hazards introduced through greater functional variability than in *hamatum*.

The two species differ strikingly in their pattern of raiding. Both operate on chemical traces deposited in relay fashion by ants in the advance, but many differences exist in the way the traces are used. In *burchelli*, the raid basically involves a large unitary body or swarm of ants in the advance, which on nomadic days may approach 20 meters in width before it divides (15), whereas *hamatum* operates from branching columns with small groups of ants foraging at the termini of the newest trails (13, 14).

In the large *burchelli* swarm or its later sub-divisions, in contrast to the many small raiding groups at the ends of *hamatum* branch trails, striking differences are seen as well as similarities. Both species form new chemical traces extending the chemically saturated raiding area; both make extensive

use of tactual stimuli. But the longer distances over which "pioneers" advance in the *burchelli* raid, and their typically more rapid progress, contrast with the slower, more hesitant advance of successive "pioneers" in *hamatum*, over only a few centimeters as a rule. In *burchelli*, the foragers extend their odor traces over an area, in *hamatum* along a linear, canalized pathway. In *burchelli*, at any one time, direct liaison in the raid is maintained over a far greater area than in *hamatum*, in which the many foraging groups are connected indirectly through basal columns (Figure 1).

The communication pattern of the raids is thus very different in the two species. *Burchelli* forms a massive body of workers, many meters wide but only one or two meters deep, which sweeps broadside forward as a single pillaging body. Behind this swarm as it advances there is left a long fan-shaped network of columns narrowing down to a single wide column communicating with the bivouac in the rear. In the raids of *hamatum*, each of many small advance groups leaves in its wake a single narrow column, from which the bivouac may be reached over older branch trails in the rear. In *burchelli* the foragers, over their basal trails, carry back to the temporary nest a much wider variety of prey than in *hamatum*. The booty of raiders in *burchelli* includes the torn-up bodies of many arthropods, large and small, unable to escape the rushing attack of the foragers and the quick, excited darting upon what excites them by movement and by odor. They also take the soft-bodied brood of ants and other insects, which is almost the only booty of *hamatum* from its slower, probing advances. Only when most excited, at the beginning or near the end of the nomadic phase, does *hamatum* capture adult insects, and even then it is limited to smaller types such as ants. The prey of *hamatum* thus contrasts sharply with the large, adult arthropod material caught and dismembered by *burchelli* even in the least excited raids of the statary phase.

The characteristic species differences in raiding are due in part to the fact that in *burchelli* the workers are more excitable and are more readily drawn stimulatively from their bivouac into a raid, also to the fact that group activities in this species are facilitated through intensive chemotactical communicative processes across occupied areas rather than along canalized routes as in *hamatum*. These gross differences between the species seem referable to basic differences in individual sensitivity, excitation level and reactivity, indicated in Table I. Among the many detailed differences, corresponding types in the polymorphic worker series of *burchelli* are larger and stronger, thus able to attack and overcome larger prey when aroused than can *hamatum*. Such advantages, together with the more virulent stinging and stronger biting of *burchelli*, make for effective mass attacks in contrast to the probing tactics of *hamatum*. Basic to the activity pattern of *burchelli*, however, are characteristics of reactivity contributing to group facilitation processes rising more rapidly to more intensive activities by greater numbers than in *hamatum*. *Burchelli* soon covers its prey with attacking masses, and readily forms heavy groups or interconnected chains of workers, efficient for stretching and

tearing it apart. Workers of this species advance and attack sources of movement stimulation sufficiently strong to cause all workers except the largest in *hamatum* to retreat. *Hamatum* forms its largest terminal groups and captures adult insects at times in the nomadic phase when colonies are at their highest pitch of excitement. Even then, their greatest arousal scarcely approaches that normal for *burchelli*, the workers of which have a distinctly lower threshold of excitation and a wider scale of reactivity.

Burchelli behavioral characteristics tend to be more intensive and massive than those of *hamatum*. Their collective odor, perceptible to man as heavier, more pervasive and often distinctly fetid, contrasts with the lighter, more fragrant odor characteristic of *hamatum*. We know these odors, and the trail-secretions of the species, not as yet in biochemical terms, but rather as traces to which the ants react. And worker reactions to the trails justify our thinking of the trail-secretion of *burchelli* as heavier and more diffuse, that of *hamatum* as lighter and more restricted linearly. The queen odors as well as the brood odors of these species seem to differ comparably. There are many indications that in their olfactory thresholds as in their excitatory processes generally, and in their secretory and reactive properties, members of the community in *burchelli* are specialized in relation to a wider scale extending to greater magnitudes than they are in *hamatum*.

With respect to habitat, both of these species are found typically in tropical forest or near it, and seldom invade open areas for long. Both are epigaeic, raiding and nesting extensively above ground. However, as laboratory tests show, *burchelli* is more readily and effectively adapted to brighter light than is *hamatum*. Under fairly intense light, foragers in *burchelli* operate more freely in the open, running less beneath leaves and other cover in raids than workers in *hamatum* at equivalent stages in the functional cycle. A greater toleration of bright light may account in part for the fact that workers in *burchelli* operate higher in the vegetation and hence at points higher in the vertical light-intensity gradient than in *hamatum*. Reactions of workers of the two species in light-susceptibility tests when eyes are covered indicate that differences in infra-cuticular sensitivity to light may be involved, as well as in optic sensitivity. In *E. burchelli* the lateral ocelli are somewhat larger and have thicker single lenses than in corresponding castes in *hamatum* (27). As between these terrestrial dorylines the matter is relative; later, we shall find reasons for believing that otherwise it may be crucial for a hypogaeic as against a terrestrial adaptation.

The fact that in *burchelli* the colonies raid much higher into the vegetation and in greater numbers than in *hamatum* may prove to be complex rather than simple in its basis. As laboratory tests suggest, a greater desiccation tolerance in *burchelli* may also contribute to its superior arboreal tendency. Differences in reactivity to temperature and humidity as well as to light may be involved in certain differences in the nesting behavior of the two

species (24). Under similar conditions, and particularly in the dry season, colonies of *hamatum* form no bivouacs higher than about one meter from the ground, but occupy underground sites such as mammal burrows more frequently than *burchelli*. Although both species are dominantly epigaeic, in *burchelli* the entire ecological repertoire tends more toward the arboreal than in *hamatum*.

The complexity of these matters may be illustrated in terms of a further difference in the bivouacking of these two species. Under all conditions of season and activity phase, 18 per cent of 238 bivouacs in *burchelli* were of the "pouch" or suspended type, but only two per cent of 397 in *hamatum* (24). Contributing to this difference in nesting are factors that permit *burchelli* to invade the vegetation in greater numbers and to greater heights than *hamatum*—e.g., in *burchelli* the colonies are larger, and in the workers, summated group excitation mounts faster and carries further than in *hamatum*. But also, the workers of *burchelli* have stronger bodies and larger tarsal hooks which aid them in forming and maintaining clusters in the absence of basal support and often without internal physical support as from vines.

Still other differences of importance are indicated between the contrasting functional patterns of these species, and there may be some unsuspected ones. Interest in the process of comparison is increased when these Eciton species are compared with dominantly hypogaeic dorylines sympatric with them in tropical America. However, considerations with respect to basic differences in functional patterns among the dorylines recommend that our next comparison be one of continentally separated genera.

THE DORYLUS FUNCTIONAL CYCLE

Species typifying the African subgenus Anomma. — The driver ants of Africa, species in the genus *Dorylus*, also exhibit a regularity in their raiding and emigrations, as the study by COHIC (3) and the recent investigation by RAIGNIER and Van BOVEN (11) indicate. The general nature of the adaptive pattern in *Dorylus* may be outlined by comparing two species studied by RAIGNIER and Van BOVEN, *D. (Anomma) wilverthi* and *D. (Anomma) nigricans*. *Anomma wilverthi* will be considered first.

A. wilverthi is essentially subterranean in its nesting, forming centralized clusters usually 1-2 m below the surface as under the root masses of trees, or, less frequently, partially exposed at the surface. Its bivouacs appear to be more superficial at those times when massive colony emigrations occur. RAIGNIER and Van BOVEN find that an emigration of these driver ants is a single operation continuing day and night for two or three days as a rule, until the entire colony has shifted to a new site. On the average, the distance is about 200 meters from the previous site. Here the colony settles for a stay of from 6 to 40 days, or sometimes even longer (Figure 2),

before another emigration occurs. RAIGNIER and Van BOVEN confirm in some detail the fact noted by COHIC, that at the time a characteristic Anomma emigration occurs, nymphal worker stages nearing maturity or already eclosed predominate in the broods. These broods are enormous, calculated to number around one million individuals. RAIGNIER and

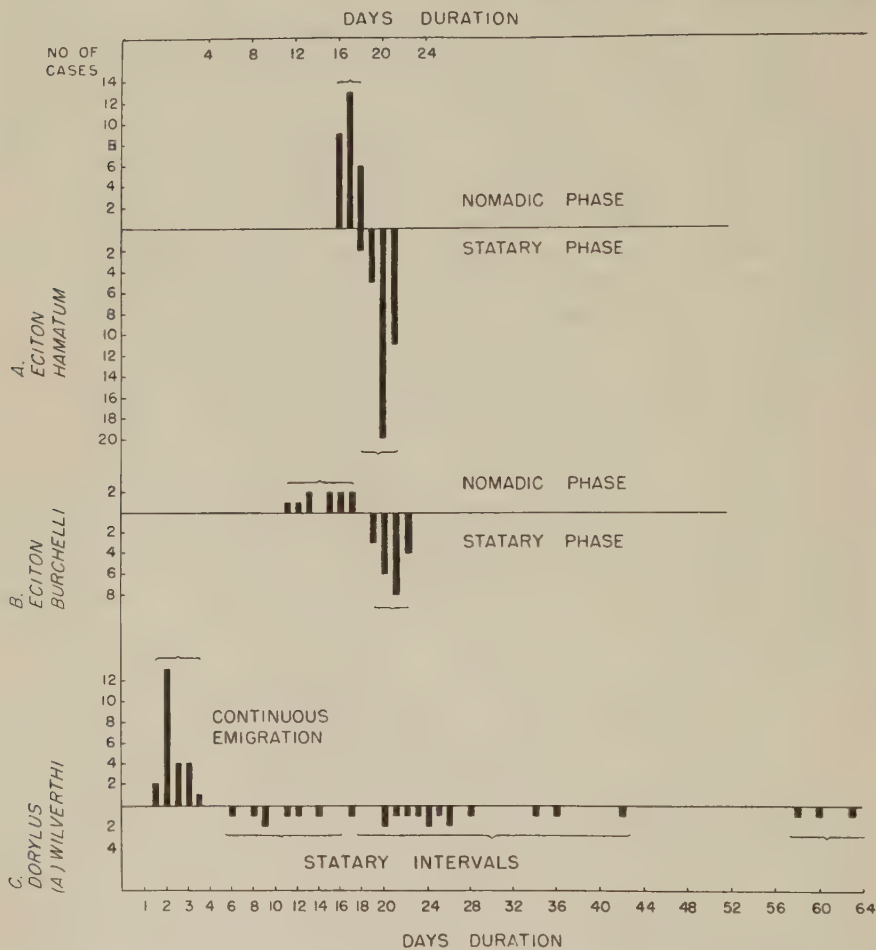


Fig. 2. — Schema of the temporal relations of fixed sojourns and colony emigrations in *Eciton* and in *Dorylus*. A—Durations of 28 nomadic phases (above) and 38 statary phases in *E. hamatum*; B—durations of 10 nomadic phases and 21 statary phases in *E. burchelli*. C—Duration of 24 different emigrations (above) and 25 sojourns in fixed locations between emigrations in *D. (A.) wilverthi*. (*Eciton*, from Schneirla; *Dorylus*, from Raignier and Van Boven.)

Van BOVEN report that one of these massive eclosions of a new worker brood occurs most frequently at intervals of 20 to 25 days, an interval also described by them as the most frequent time between emigrations. They conclude that it is this eclosion, raising the "psycho-physiological state of the colony", which determines the exodus. Therefore, they say,

« ... le déterminisme des exodes ne dépend pas de facteurs extérieurs, mais est régi par la situation interne de la colonie, par le rythme physiologique de la ponte et du développement du couvain. » (11, p. 241).

This interpretation resembles my theory of Eciton nomadism (14) at least to the extent that it postulates a basis for the emigrations of *Anomma* in reproductive processes. We shall return to the point.

These authors also report for *A. wilverthi* that in a majority of cases the queen delivers a great new batch of eggs after an emigration is completed. In about 30 per cent of their recorded cases, the prolific egg-laying episode preceded emigration, a fact to which they attribute shorter emigration intervals described as centering around 11 days (see Fig. 2). Longer intervals exceeding the described mode of 20-25 days are attributed to the presence of a brood of male larvae, the great individual bulk of which is presumed to inhibit the normal emigration-arousing effect of an eclosing nymphal worker brood. Although there is at present no explanation of the described variations in the timing of high points in the egg-laying processes of the queen in *Anomma*, the authors seem to imply that the periodicity of emigrations in these ants is due to an endogenous process governing the queen's reproductive rhythm. However, the possibility cannot be excluded that extrinsic factors may be involved in the timing of this rhythm.

Comparison of A. wilverthi and nigricans. Further characteristics of the best-known species of driver ant, *D. (Anomma) wilverthi*, may be outlined to advantage in a comparison with *D. (Anomma) nigricans*, a species studied by Conic and by RAINIER and Van BOVEN. The characteristics of these species are contrasted in Table II. In *A. wilverthi* the colonies are clearly more active than those of *A. nigricans*, in which raids are smaller and less frequent. Both species are swarm raiders, but the raiding bodies of *A. wilverthi* tend to be larger and more vigorous, as well as more productive. RAINIER and Van BOVEN found that in the base columns of *wilverthi* up to 22 per cent of the ants returning might be laden, in contrast to only about 5 per cent in *nigricans*. In *A. wilverthi* the raiders tend to be more excitable, moving faster in wider columns emptying into larger advance bodies than in the slower-moving *A. nigricans*.

A. nigricans is more hypogaëic than *A. wilverthi*. RAINIER and Van BOVEN found the former species tending to run its base columns underground twice as often as the latter, in which raiding columns run underground in only about one-fourth of the cases. A comparable difference was found in their emigration columns. Also, *A. nigricans* more frequently covers its exposed surface columns partially or completely with detritus or borders them with clusters of workers. As both species lack eyes altogether in the workers, although vestiges of optic ganglia exist, whatever role light may play in this behavior must be a matter of infracuticular sensitivity. In this respect, *A. nigricans* would seem to be the more susceptible. But the authors attribute digging, wall-building

TABLE II

COMPARISON OF *Dorylus (Anomma)* SPECIES (Based on Raignier & Van Boven, 1955)

	<i>D. (Anomma) wilverthi.</i>	<i>D. (Anomma) nigricans.</i>
Raids.	<p>Larger swarms, clearly more active than <i>A. nigricans</i>; more than one expedition often formed per day.</p> <p>Base columns average over 3 cm. in width; more crowded, ants move faster than in <i>nigricans</i>.</p> <p>Base columns underground in 22% of studied cases; digging, walling less frequent.</p> <p>Up to 22% of returning ants in base columns laden, in observed cases (6-22%, Av. 14%).</p>	<p>Smaller raids, less frequent than in <i>A. wilverthi</i>. Raidless days more common. Evidently more subterranean raiding.</p> <p>Base columns narrower, slower moving and less crowded than in <i>A. wilverthi</i>.</p> <p>Base columns underground in 46% of studied cases; digging, walling of exposed columns frequent.</p> <p>Up to 10% of ants returning in base columns laden (0.8-10%, Av. 4%).</p>
Nests.	1-2 meters deep, 3 m. sq.; compact mass formed in single central cavity, with higher ("physiological") temperature.	2-4 meters deep, dispersed in numerous deep chambers and galleries, with lower temperature.
Emigration.	<p>Continuous, long movement lasting 2-3 days, concurrent with predominance of eclosing worker nymphs in brood.</p> <p>Occurs at intervals of 6-40 days, sometimes longer; most frequent interval 18-26 days. Columns commonly subterranean at intervals, sometimes altogether.</p>	<p>Movement probably similar to <i>A. wilv.</i>, except more fully subterranean, possibly more protracted. (Seem also to concur with predominance of eclosing worker nymphs in brood,—<i>v. infra</i>.)</p> <p>Intervals probably much longer than in <i>wilverthi</i>; one case of more than 125 days observed. Columns much more frequently subterranean in part or as whole than in <i>A. wilverthi</i>.</p>
Light sensitivity of workers.	Eyes absent in workers, vestiges of optic ganglia present.	Eyes absent in workers; vestiges of optic ganglia present (may be more susceptible to infracuticular light effects than <i>A. wilverthi</i> — <i>v. infra</i>).
Queen.	Peak of egg-laying reached commonly at 20-25 day intervals.	Peak of egg-laying probably reached at much longer intervals than in <i>A. wilverthi</i> .
Workers.	<p>Allometric difference: cephalic index (head-shape) less than 100 for workers of all sizes.</p> <p>More active, excitable,—probably have higher metabolic rate than <i>A. nigricans</i>.</p>	<p>Cephalic index increases with worker size and can exceed 100.</p> <p>Slower-moving, less excitable; probably have lower metabolic rate.</p>

and clustering with reference to trails simply to the existing condition of "excitation" in the workers, excluding a relation to the effect of light. However, as suggested above for *Eciton*, these hypotheses are not mutually exclusive. Actually, it is to be expected that both level of excitability and sensory susceptibilities are involved and usually interrelated in determining species differences in reactions to external situations, as well as intra-species differences under different conditions.

Of great interest is a characteristic difference in nesting reported by RAINIER and Van BOVEN. Colonies of *A. nigricans* tend to cluster deeper in the ground and to disperse more widely in chambers and galleries than colonies of *A. wilverthi*, in which the population typically forms a compact mass in a single central cavity nearer the surface. Within this central mass, a higher (physiological) temperature prevails than in the more scattered nesting aggregations of *nigricans*. Although RAINIER and Van BOVEN were able to carry out only three continuous studies with colonies of *A. nigricans*, one of these colonies held the same nesting site for at least 125 days,—an interval more than twice as long as the longest nesting stops in *A. wilverthi*,—the other two for more than 45 days. The inter-emigration intervals of *A. nigricans* seem to be typically much longer, and as the authors suggest, the basis seems to lie somehow in the lower nest temperatures of *A. nigricans*.

The findings of RAINIER and Van BOVEN show clearly that in *A. wilverthi*, emigrations occur coincidently with massive nymphal eclosions. For *A. nigricans*, on the other hand, their limited evidence is inconclusive although indicative of the same relationship, as was that of COHIC (3). Fortunately, during the past ten years three clear cases bearing on this point have come to my attention. All of these cases, reported from widely separate parts of Africa, involved colonies of *D. (A.) nigricans* in which the brood was sampled extensively at the time of emigration. One was studied in 1946 at Nyomeni, Tanga, by Dr. R. G. H. SWEENEY and involved *A. nigricans burmeisteri* var. *rebellus*, the second by Dr. Boris MALKIN in 1949 at Kabetz, Victoria, British Camerrons and involved *A. nigricans burmeisteri*, and the third was observed in 1953 at Ibadan, Nigeria by my colleague, Dr. L. R. ARONSON, and involved *A. nigricans arcens*. In each of these cases, a predominance of mature worker nymphs was clear in the very large brood samples sent to me by the finders. Dr. Van BOVEN kindly made the identifications.

The two species appear to be similar in another respect, despite the striking difference that evidently exists in their inter-emigration intervals. Although RAINIER and Van BOVEN reported no direct evidence on egg-laying by the queen in *A. nigricans*, one of the above cases bears specifically on this point. The colony of *A. nigricans arcens* found by Aronson was in full emigration when first observed, and on completion of the movement a few hours later was found to have established itself in a closed cavity near the surface in hard, laterite soil. Several hours after the emigration had ended, the queen was taken from the center of the largest cluster, in

a moderately physogastric condition and laying eggs at the time. Fortunately, with the aid of Dr. J. E. WEBB of The University College, Ibadan, it was possible to fix this queen in Bouin's solution shortly after her capture. Dr. Roy WHELDEN of the Haskins Laboratory, Union College, who submitted the specimen to a detailed anatomical and histological study, calculated that her ovarioles contained at least 500,000 eggs in a generation roughly at maturity. A minor part of this brood had been laid prior to capture, and there can be little doubt that, if she had not been taken away, this queen would have laid most or all of the large remainder in a continuous operation. This case indicates that in *A. nigricans* the principal part of an egg-laying episode may occur directly after an emigration has been completed. Conditions in *A. nigricans* therefore resemble what seems to be the rule for *A. wilverthi*, with respect to the time at which egg-laying may occur.

However, from the findings of RAINIER and Van BOVEN it seems probable that *A. nigricans* has longer inter-emigration intervals than *A. wilverthi*, and that the queen of *nigricans* has her peaks of egg-laying at longer intervals than the queen of *wilverthi*. This difference they attribute to the prevalence of a deeper nest in *A. nigricans*, with the nesting clusters more scattered and lacking the higher temperature prevalent in the nests of *A. wilverthi*. This suggestion is consistent with an explanation advanced by us (20, 24) to account for the relationship between bivouac microclimatic conditions and time relations in the functional cycles of Eciton species. Although the principle is much the same, it is clear that the difference between *A. wilverthi* and *A. nigricans* in their inter-emigration intervals is far greater, and far more variable, than that between Eciton *burchelli* and *hamatum* in the duration of their nomadic phases.

RAINIER and Van BOVEN attribute the periodicity of emigration in the Anomma species studied by them to "the physiological rhythm of laying and the development of the brood". Although this general statement is probably true as far as it goes, I believe that a more specific conception of the causal nexus may be obtained through a comparison of the drivers with the army ants.

COMPARISON OF ANOMMA AND ECITON

General similarities and differences. — It is clear from the general circumstances reported in Table III that both *Anomma* and *Eciton* are similarly adapted on a nomadic, predatory basis probably by virtue of common ancestry. However, from present similarities and differences, it is not easy to discern what may have been retained from the hypothetical predoryline ancestor and what may have evolved since their lines became separated.

Both groups are carnivorous. Although in the terrestrial Ecitons the proclivity for a carnivorous diet seems to be thoroughgoing, in *Anomma*

there is a distinct indication of a partially vegetarian diet, extending to seed pulp and other plant material, as Green (6) reported for *Dorylus* in India. Evidence of a limited vegetarian departure in some of the hypogaec dorylines of the New World (29) suggests that a subterranean pattern of life may involve factors extending the diet beyond animal tissue.

Both *Anomma* and *Eciton* carry out massive predatory forays. These both resemble what I have termed the *swarm-raid pattern* (15). The collective foraging expeditions of *D. (A.) wilverthi* and of *E. burchelli* are superficially much alike, with their great advance foraging bodies from which captured prey is carried over narrow columns to the temporary nest in the rear. In the prey of both, dismembered arthropods predominate with insect brood also present. In both, individual forays usually begin by a radial spreading of ants from the nest center, with a unitary body forming on one side when ants are drawn from other quarters into the part that has begun to move most rapidly outward. The communicative integration within the organizing mass seems to involve in both cases a complex tactual-olfactory process similar to that I described (15) for *burchelli* as *drainage*. Although RAINIER and Van BOVEN refer to this similarity only with respect to column situations in *wilverthi*, they also mention a related but different process which I found very important for integration in the mass maneuvers of *burchelli* and conceptualized as *pressure*. However, in the mass operations of *wilverthi*, which appear to be more diffuse and irregular than those of *burchelli*, the processes of intra-group integration through pressure and drainage may be slower and less regular than is typically the case in the *burchelli* swarm. Further comparison of these phenomena is of interest in relation to problems of mass communicative processes in social insects.

Although both major types of correlation process, pressure and drainage, seem to be involved in the mass raids of *Anomma* and of *Eciton burchelli*, the resulting integrative processes appear to be somewhat different in detail. In contrast to the swarm of *E. burchelli*, which in its first hours of operation typically holds well to one general direction without major continued deviations of more than 15° as a rule (15), in the advance of an *Anomma* swarm RAINIER and Van BOVEN find much variability in the direction of progress. In the raid of *burchelli* a broad and relatively shallow advance mass maintains an impressively regular forward advance and is promptly reconstituted as a rule after occasional disruptions such as expeditions in force up great trees. The persistence of a typical pattern and direction of operation in the *burchelli* swarm through its first hours is based upon the steadying and directionalizing effect of an integrating factor operating from outside this body. This is a constant intense *pressure* distributed through the fan broadside against the base of the swarm, and exerted against the rear of that body through the constant arrival of masses of ants from the an. In relation to and in dependence upon this factor, correlation processes go on within the mass which make it an organized body. The presence of an effective internal organisation,

TABLE III

Anomma (Raignier and Van Boven) and *Eciton* (Schneirla) COMPARED.

	<i>Anomma.</i>	<i>Eciton.</i>
Colony populations.	20-22 millions est. in <i>A. wilverthi</i> .	300,000 to 1 million or more est. in <i>E. burchelli</i> ; 250,000 or fewer in <i>hamatum</i> .
Habitat.	Tropical forests to open areas, savannah; distinct subterranean tendency.	Tropical forest largely, with open areas infrequent, incidental; epigæic, terrestrial adaptations.
Nesting.	Subterranean clustering for many days, closer to surface at emigration times; much secondary modification of site through digging.	Exposed clusters above surface; often arboreal in <i>burchelli</i> . Sheltered, even subterranean in statary phase. Essentially no modification of physical situation occupied.
Colony activity schedule.	Related in general to brood condition; indistinct relation to light-dark rhythm.	Specific, relatively precise relationship to brood condition; also to light-dark rhythm.
Raiding.	Diet mainly carnivorous; dismembered arthropods, largely; occasional fats, vegetables. Raids begin at any time of day or night, more frequently early at night; duration variable, up to 20 hours.	Exclusively carnivorous diet; dismembered arthropods in <i>burchelli</i> , mainly insect brood in <i>hamatum</i> . Raids begin at daybreak, cease at dusk (more variable in statary phase, with later morning, early afternoon starts).
Raiding pattern.	Advance swarm, variable in width (ca. 12 m.) and depth, narrowing irregularly to consolidation columns. Swarm advance variable in direction; av. rate 20 m./hr.; swarms probably much larger in population than in <i>burchelli</i> . Up to 22% of returning ants laden in <i>A. wilverthi</i> , fewer in <i>nigricans</i> .	Advance swarm in <i>burchelli</i> , up to 20-25 m. wide, 1-2 m. deep; distinct fan of columns behind, narrowing regularly to one column. (Branching-column pattern in <i>E. hamatum</i> .) Swarm advance fairly direct in morning; alternating swings; rate ca. 20 m./hr.; probably a larger part of population raids. Percentage of laden ants larger but variable; often greater than 50%.
Emigration.	Single movement, usually lasting 2-3 days, continues day and night. Occurs when mature worker nymphs predominate in brood. Exodus distance (M = 223 m.).	Continuous movement, but each emigration completed in a single night during the nomadic phase. Distinct relationship to brood condition; occurs when callows or growing larval brood present. Mode = 140 m. in <i>E. burchelli</i> , 225 in <i>hamatum</i> .

TABLE III (CONT.)

	Route extensively subterranean, covered surface runways; queen may be mainly dragged.	Column fully exposed on surface; queen runs fully under own power.
Cycle.	Emigrations most frequent about 20-25 day intervals; stable nests intervene (Raignier & Van Boven deny nomad-statory cyclicality).	Distinct nomad-statory cycle; in <i>burchelli</i> , nomadic 12-15 days, statory 21 days; nomadic phase more precise in <i>E. hamatum</i> .
Queen.	Single colony queen (approx. length, head to gaster, <i>ca.</i> 40-50 mm.; gaster, 19-45 mm.)	Single colony queen (approx. length in <i>burchelli</i> , head to gaster, 21 mm.; gaster 10 mm. contracted, 21 mm. physogastric).
	Continuous moderate physogastry, egg-laying may be discontinuous, with peaks at 20-25 day intervals in <i>wilverthi</i> .	Distinct alternation of non-laying contracted condition with physogastric, laying condition, <i>ca.</i> each 34 days in <i>burchelli</i> .
	Egg-laying usually intensified just after emigration; in 30% prior to emigration; eggs not in separate batches (11), estimate 3-4 million laid per month. (14,000 ovarioles in <i>D. (A) nigricans arcens</i> —R. W. Whelden).	Eggs laid midway in each statory phase, in distinct batches of 130,000+ in <i>burchelli</i> (2,600 ovarioles in <i>burchelli</i> —H. Hagan,—9).
	Intensification of egg-laying in <i>wilverthi</i> lasts 5-6 days, length of total interval unknown.	Peak of egg-laying 2-3 days long, egg-laying episode lasts <i>ca.</i> 7 days in <i>hamatum</i> , 9-10 days in <i>burchelli</i> .
	Refertilization may occur frequently during year (11).	Queen re-fertilized probably no more than once annually.
Broods.	Relatively distinct all-worker broods of <i>ca.</i> 1,000,000 individuals each.	Distinct all-worker broods, of 130,000 + individuals in <i>burchelli</i> , eclosed at <i>ca.</i> 34-day intervals.
	Males may occur in broods with workers; queen production unknown.	Males in distinct broods, around 3,000 in <i>burchelli</i> , with <i>ca.</i> 6 queens, no workers.
	Developmental period: 20 days est. in <i>wilverthi</i> for workers; 40-52 for males, laying-to-eclosion.	Development: <i>ca.</i> 45 days in <i>burchelli</i> , 47 in <i>hamatum</i> , for worker brood; 41 days both species, for male,—2-3 days less for queen.
Brood-stimulative functions.	Maturation of nymphal worker brood sets off single continuous exodus; larval-stimulative factor denied by Raignier & Van Boven. Effect of male larvæ some: how inhibits emigration, accounts for long nest stays (11).	Eclosion of pupal worker or sexual brood initiates nomadism, then wanes and larval-stimulative factor maintains phase to its end. Stimulative effect of sexual brood (males, queens) much like that of worker larvæ, as basis for nomadic phase.

despite seeming chaos, is indicated by the fact that the swarm as a unit carries out partial swings alternately to one side and then to the other at regular intervals (15). These flanking movements, analyzed in detail, reveal a regular and facile interaction of sub-sections in the general mass, through pressure and drainage processes welding it into a surprisingly efficient unitary body. Although similar processes may be inferred for the *Anomma* swarm, the matter remains to be investigated. From the description of RAINIER and Van BOVEN, which indicates that the swarms in *Anomma* are typically more irregular in pattern and inconstant in direction than those in *burchelli*, it may be gathered that the integrative processes are more sluggish, diffuse and variable in the case of *Anomma*.

The looser coordination of the *Anomma* swarm may be attributable in part to the fact that the concentration of individuals is much greater, in keeping with a considerably greater total population than in *burchelli*. Considerably greater numbers of individuals brought to bear upon a center of disturbance may account for a more rapid tearing up of prey than is usual for *burchelli*, and for the occasional inclusion of mammals among the victims of *Anomma*. However, the suspected differences in mass operations cannot be simply a matter of greater numbers in *Anomma*, but must be related to basic individual characteristics making for differences in mass behavior in the two genera. Although orientation is non-visual and proximal in both cases, generic differences in factors such as afferent thresholds, summation, reaction time and the like in responses to tactual and olfactory effects transmitted through masses of ants could account for wide differences in the mass behavioral processes. Comparable differences are to be inferred between *E. burchelli* and *Labidus praedator*, the latter with smaller raiding masses which are in general looser in organization and more variable in directionalization than those of *burchelli*. Indeed, in individual and group behavior, except for the aspect of group magnitude, the workers of *Labidus praedator* and *Anomma* seem to resemble each other more closely than either resembles *burchelli*.

With their swarm-raiding patterns broadly similar, *Anomma* and *E. burchelli* are much more alike than either is like *E. hamatum* with its column-raiding pattern. Fragmentary evidence suggests that in the Old World genus *Aenictus* a column-raiding pattern is approximated, resembling that of *hamatum* but very unlike the *Anomma* swarming pattern. *Aenictus* is reported (5) to be definitely more terrestrial in tendency than *Anomma*, a fact which together with the fixity of the swarm pattern in the terrestrial *E. burchelli* suggests the lack of any important relationship between either the terrestrial or the subterranean tendency and any one type of raiding pattern. In the New World, the strongly hypogaecic *Nomamyrmex crassicornis* exhibits in the surface-exposed portions of its raids a branching-column pattern much like that of *E. hamatum*, as does also the hypogaecic species *Neivamyrmex pilosus*, a considerably smaller ant. The principal divergence, as laboratory tests indicate, may be that individuals of column-raiding species differ uniformly from workers

of swarm-raiding species in their stimulus thresholds and excitation ranges in ways bearing not only upon the strength and timing but also the nature of response. Workers of *E. hamatum* generally are more delicately reactive to single light encounters with colony mates, and retreat at lower intensities or after less summation of environmental or group stimulation than corresponding worker types in *burchelli*. In these respects *E. hamatum* and *Nom. crassicornis* workers are alike, with the latter even more prone than the first to retire on slight disturbance, and both are strikingly different from workers of *E. burchelli* or of *Labidus praedator*. Among Old World dorylines, *Aenictus* workers may resemble those of the first American group, *Anomma* workers those of the latter, more closely.

As mentioned above there is a relatively close similarity between the swarm-raiding dorylines in their typical prey. The swarmers, with their high excitability, their tendency to advance toward relatively intense stimulation, and their bodily strength, commonly capture and dismember a wide variety of prey among the arthropods. The column raiders, in contrast, usually take soft, immobile booty such as insect brood. *E. hamatum*, when at its maximal colony excitation level in the first and the last days of the nomadic phase, often takes adult ants as prey; *burchelli*, in its least excited colony condition in the statary phase takes its lowest proportion of arthropod adults and its highest proportion of brood. This suggests that the species normally differ in what may be termed "level of excitation", with *hamatum* lower, *burchelli* higher. *E. burchelli* resembles *hamatum* far less and *Anomma* more in its range and type of prey and its general style of attack, presumably because of a closer similarity to the latter in the sensory thresholds and the reaction properties of its workers.

Environmental adaptations in Anomma and Eciton. — The *Ecitons* have in common a pronounced epigaeic tendency both in raiding and nesting, in strong contrast to the more hypogaeic *Anomma*. The activities of an *Eciton* colony are attuned first of all to the diurnal light rhythm: its raids begin in response to the first light of day, run their course through the day in a general relation to the march of environmental (e.g., light, atmospheric) events, and stop at dusk to be succeeded by a general return to base in the statary phase or by a stereotyped exodus in the nomadic phase (14, 15). A close *kinetic* responsiveness to surface conditions, and particularly to light and temperature, is apparent in the species of this genus. That *Eciton* evolution has progressed in close relation to conditions centering around the light-dark rhythm is emphasized by the existence of factors (e.g., reproductive) holding colony population magnitude in this genus within a range permitting *a complete emigration within a single night*.

The case is very different with *Anomma*, which raids day and night and which requires two or three days for its continuous colony emigration. The colonies of *Anomma* are much larger than those of *Eciton*, as are the

broods. *Anomma* raids evidently can begin at any time around the clock, although the greater frequency of starts in early evening reported by RAINIER and Van BOVEN suggests a stimulative effect of some kind related to a recovery from daytime conditions. Although different in its immediate behavioral setting, this effect may be somewhat equivalent (as in its physiological basis) to the regular *Eciton* resurgence of raiding activity in early afternoon following the midday "siesta" effect (14, 15). In *Anomma* also, midday environmental conditions evidently exert a drepressing effect, which however has a different relation to the course of extra-bivouac activities than in *Eciton*. This is indicated by the fact that, according to RAINIER and Van BOVEN, a great proportion of the raids started in the early evening of one day come to a stop just before noon on the next day. In *Eciton*, only an occasional weak raid in the statary phase will be stopped in this manner.

The fact that *Anomma* workers are eyeless, whereas *Eciton* workers have developed lateral eyes, suggests the importance of a photokinetic factor in the timing of the clear-cut daily routine of *Eciton* colonies. The valuable histological study of WERRINGLOER (27) showed that the eyes of the American dorylines, an interesting type of degenerate single-lens compound eye (a "lateral pseudo-ocellus", as WERRINGLOER called it) are largest with best developed neural connections in epigaeic species such as *Eciton burchelli* and least developed in the most hypogaeic, as in *Labidus coecus*. The promptness and vigor with which the nomadic raids of both *E. burchelli* and *hamatum* start at daybreak, in contrast with latency and delay in the statary phase (15), clearly indicates a relationship between behavioral tonicity and light. That this effect is to an extent visual is indicated by the unresponsiveness of groups of *Eciton* workers with covered eyes when exposed to *faint* light (even after dark-adaptation, and with temperature controlled) in the laboratory. In the *Ecitons*, thermokinesis functions similarly to photokinesis, but is secondary. In *Anomma*, an arousal pattern in which non-photoc factors dominate is clearly inadequate for the appearance of any but a variable diurnal routine quite unlike that of the precise dawn-to-dusk raiding program and the nighttime exodus of the *Ecitons*.

What permits the *Ecitons* to live a mainly terrestrial life, but limits the *Anommas* greatly in this respect, is undoubtedly complex. It cannot be the optic aspect alone, although Werringloer's evidence reveals an interesting parallelism between the relative epigaeic tendency on the one hand and the development of the lateral pseudo-ocelli and their neural connections on the other. *Eciton burchelli*, most strongly terrestrial and even arboreal among the American dorylines, has the best developed optic system, with *E. hamatum*, terrestrial but less arboreal, next, and last the species *Labidus mars*, strongly hypogaeic and the only American doryline known to be altogether eyeless in the workers. Laboratory tests on the responses of workers in *E. burchelli* and in *Labidus coecus*, the latter almost without eyes and strongly hypogaeic, suggest that mechanisms enforcing strong

phobic responses to light and other surface radiation are involved in keeping the hypogaecic species down. Even with eyes effectively covered, the workers of *Labidus coecus* continue to show stronger disturbance in a field of intense light, and to assemble much sooner in a dark zone into which they can wander, than *E. burchelli*.

These results, together with the fact that an inverse relationship exists in the American dorylines between strength of hypogaecic tendency and the development of visual equipment, suggest that irritation by light through non-visual infracuticular mechanisms may play a basic role in the subterranean tendency. It is interesting to note that workers of *Anomma* species, although quite without eyes, are clearly reactive to and often greatly disturbed by light. With light-sensitive equipment must also function other mechanisms, as yet poorly known, favoring a life based upon nesting in the soil.

It is probably that conditions of greater irregularity in forest cover prevailed when the Old World dorylines attained their dominantly hypogaecic pattern, in contrast to a continuity of heavier forest cover in the New World tropics affording conditions under which the Ecitons could evolve to a specific epigaecic adjustment.

Adaptation to surface conditions in *Eciton* has been aided greatly by mechanisms underlying the unique unitary bivouac cluster of these ants (11); in fact we have found the bivouac fundamental to this epigaecic doryline pattern (24). Because the bivouac affords a highly stable microclimate for the colony and its brood, the Ecitons are the most regular of all known dorylines in the conditions of their brood development. This characteristic is evidently crucial for their highly regular cyclic behavior pattern, involving a life of greater mobility at a consistently higher metabolic tempo than is known for any hypogaecic species. In its one periodic emigration, roughly at three week intervals, a colony of *A. wilverthi* moves on the average only 250 meters (11), in comparison with which a colony of *E. hamatum* moves 16 or 17 times on successive nights in one nomadic phase, or at least ten times as far in the same time interval (20). *E. burchelli* is similarly much more mobile than *Anomma*, and this type of regular mobility in space seems most highly developed in the epigaecic Ecitons, of all dorylines. Many factors contribute.

The Eciton bivouac cluster is not fixed in the soil, but is open to the atmosphere during the nomadic phase. As we have found (24), it is capable of facile structural changes through worker responses to external conditions, so that the internal microclimate is efficiently stabilized despite wide external variations through the day. Its structure, also readjusted rather delicately in relation to the condition of the brood, involves an internal temperature gradient of constant direction although variable in detail (9a). It is important to note that the smallest brood members are regularly situated centrally where the high point of the gradient prevails, the largest members peripherally (24). In effect, these conditions permit a regular differential in the growth rate of the brood, whereby

the range of time at egg-laying is reduced at later stages, as relative growth is most rapid in the potential workers minima, developing from last-laid eggs, least rapid in the potential workers major developing from first-laid eggs (25). This fact must be held important for the efficacy of the brood's stimulative role in the colony functional pattern (22). In *Eciton*, the brood-stimulative effect is strong not only at pupal maturity and eclosion, but also throughout the greater part of larval development to maturity. In *Anomma*, on the other hand, a relatively smaller differential may prevail in the growth rate of different castes in the brood during the larval stage, presumably ruling out a brood-stimulative impact sufficiently strong to account for emigration at this time. It is evidently a fact for *Anomma* that the total stimulative effect of a larval brood on the population is not in itself a sufficient cause for emigration (11, 22).

Along these lines, a significant difference seems indicated between *A. wilverthi* and the deeper nesting *nigricans*. The former, as RAIGNIER and Van BOVEN have shown, nests closer to the surface in a compact mass in which a higher central temperature prevails than in the deeper situated, more diffuse nest aggregations of *A. nigricans*. This condition in *wilverthi* no doubt contributes to the more rapid brood development reported, as well as to a higher metabolic rate as basic to colony activities in that species. The frequency of emigration in *wilverthi* (Fig. 2) seems to be considerably greater than that in *nigricans*, also the general rate and vigor of colony function is correspondingly much higher. In similar terms, *Eciton* species evidently exist on a still higher metabolic level than *A. wilverthi* and other *Dorylus* species, by virtue of surface-adapted mechanisms such as their form of bivouac which augment the efficiency and precision of reproductive functions basic to nomadic life.

This difference in the pace of life is clearly represented by the prevalence in *Eciton* of an intimate relationship between the *daily* raid of the nomadic phase and the *nightly* emigration as its direct outcome (14, 15), in contrast to a far more variable relationship in *Anomma* (11). In *Eciton*, the emigration occurs as a direct sequel to the raid, as a different pattern of colony behavior arising at a lower level of excitation. When the daily fall in light intensity to effective zero at twilight accounts for a greatly depressed activity level in the workers, responses to external conditions fall correspondingly in variety and scope, becoming stereotyped mainly in terms of highly canalized reactions to the chemical trail and to nestmates. The adaptive relations of colony behavior then depend upon central stimulative sources affecting the general excitation level of the worker population. The relationship between extrinsic conditions and the intra-colony situation seems to be simpler and less specific in *Anomma*.

Reproductive function and cyclic behavior in Anomma and Eciton. — The evidence for *Eciton* indicates very clearly that in this genus the brood plays a major role in the determination of cyclic variations in colony function.

In the statary phase, when the advanced brood is enclosed in cocoons, quiescent and least stimulative to the adult population, each diurnal raid is small and ends in a general return to the bivouac with booty after night-fall, instead of exodus. In the nomadic phase, on the other hand, the presence of newly eclosed callows or of a highly stimulative larval brood accounts for much larger raids and for a persistence of traffic pressure from the bivouac even after dusk. Then, with the failure of daylight, the raiding population drains into one central avenue of exodus (a former principal raiding trail), heaping booty in existing caches at trail junctions. These points inevitably become feeding centers for larvae deposited there during traffic blockages, or (early in the nomadic phase) for callows, which are notable blockers of traffic. Such traffic impedances are not only important factors in the development of an emigration (13, 14), but also serve to augment the stimulative and nutritive processes of the colony appreciably. No such direct relationship between raiding, emigration, and colony trophic processes seems to hold in *Anomma*.

Circumstances indicate that brood relationships with the adult population may be less intimate and also more variable in *Anomma* than in *Eciton*, particularly as concerns the larvae. Even so, I believe that the concept of a trophallactic relationship, centering around reciprocal stimulative processes involving tactual and chemoceptive effects, as in the theory I advanced for *Eciton* in 1938 (14), may hold substantially for *Anomma*. RAIGNIER and Van BOVEN, in the absence of direct evidence, seem to prefer more general expressions such as "internal state of the colony" and "physiological rhythms of egg-laying and of brood development" for causes underlying emigration. But it is probable that in *Anomma* also the causation of nomadism may be carried beyond the reproductive cycle to aggregate excitatory effects of brood dependent thereon as the critical intervening factor.

From the facts reported by RAIGNIER and Van BOVEN for emigration and for the inter-emigration intervals in *A. wilverthi*, it is apparent that the intervals of nomadism are much shorter, the inter-emigration intervals more variable and frequently much longer than in *Eciton* (Fig. 2). It is perhaps this difference in time relations, first of all, that leads these authors to the conclusion, with reference to the causation of emigration in *Anomma*, that:

« Ce déterminisme, tout en étant de la même nature (cycle reproducteur) est tout de même fort différent de celui qu'à découvert Schneirla chez les *Ecitons*... D'abord, il n'y a pas d'alternance de périodes sédentaires et nomades. » (11, p. 241.)

However, I believe that from the findings of these authors themselves, the concept of a functional cycle with alternating nomadic and statary phases is applicable to *Anomma* in a manner comparable to *Eciton*, and very possibly on a homologous basis. The gist of the results is presented in Figure 2. On grounds of functional equivalence to *Eciton* each of the periodic emigrations reported for *A. wilverthi* may be considered a *nomadic*

phase, and the nesting stop of short or longer duration preceding the next emigration may be considered a *statory phase*. No matter how short or how long these two different types of interval may be, they recur alternately, and each involves colony behavior differing characteristically from that of the other but related to it, analogous to the state of affairs in *Eciton*. Also, as in *Eciton*, these two behavioral episodes involve a cyclic pattern of alternating functional conditions in the colony, with reproductive processes as the basis.

For reasons much the same as those I have advanced for *Eciton* (17, 18), this behavior pattern represents a case of migration, not only because reproductive processes are basic to it, but also because the intervals of emigration (nomadic phases) involve a recurrent return to environmental conditions differing characteristically from those of the statory phase. *Eciton* colonies differ clearly in their ecological situations in the nomadic and statory phases. In *Anomma* also, certain recurrent differences in environmental adjustments, comparable to those of *Eciton*, are indicated. For example, prior to the occurrence of an emigration, colonies of *A. wilverthi* rise closer to the surface in their subterranean nesting situations, somewhat as colonies of *Eciton* emerge more and more from their enclosed bivouac sites during the final days of a statory phase. It is this capacity for alternating between ecologically different situations, as well as a basis in reproductive processes, that justifies considering the *Eciton* nomad-statory cycle a case of migration. Despite obvious differences as in timing, I believe that the *Anomma* pattern also conforms to this principle.

Of course, many differences exist, but these may be secondary. The longer nest stays of *A. wilverthi* are attributed by RAINIER and Van BOVEN to the presence of a male brood, the great bulk of which is presumed to inhibit an emigration in some manner despite the presence of a mature brood of worker nymphs. This seems to represent a distinct difference from *Eciton*, in which with a sexual brood the larval and eclosion-excitatory effects are equivalent to those of a worker brood, and account for the usual changes in the colony functional cycle, differing only in time relations. It is true that the male larvae of *Anomma* are much larger than those of *Eciton* (when mature, 3.5 cm. in length, as against 2 cm. in *Eciton*) and also would have to be moved up from underground, hence it is conceivable that they might inhibit an emigration through transport difficulties. On the other hand, the failure of emigration in their presence may prove to have some other cause.

Although the findings of RAINIER and Van BOVEN (cf. Fig. 2) indicate a wide variation of nest stays in *Anomma*, these authors settle upon a period of about three weeks as the normal interval, and attribute this to a 20-day frequency of egg-laying in the queen. The pattern of greatest frequency seems to involve an intensification of egg-laying just after an emigration. The maximal laying episode would seem to occur independently of the emigration itself, in view of the fact that in about one-third of the cases it precedes the exodus. Nevertheless, the authors conclude

that the exodus depends on the laying, as this brood matures in about 20 days. We may take this to mean the *previous laying*, from which arose the brood now present as mature nymphs. Our first question here involves what specifically determines the exodus.

For a valid comparison, we must ascertain what occurs in *Eciton* and in *Anomma* when nomadic behavior arises after a statary interval. In this respect, RAIGNIER and Van BOVEN seem to base their argument for a major difference between these dorylines upon a misconception. Prefatory to denying the existence of a nomad-statary cycle in *Anomma*, these authors attribute to me the conclusion that a nomadic phase is initiated in *Eciton* by

« ... un appel croissant des larves à la nourriture. » (11, p. 241.)

Unfortunately, this statement is contrary both to the facts reported and to the interpretation I have consistently advanced for *Eciton* (14, 16, 18, 20, 22). As to the facts, for *Eciton* I have demonstrated the concurrence of the eclosion of a mature pupal worker (or sexual—23) brood and the onset of a nomadic phase. As to theory, I have held on good grounds that the stimulative effects energizing the *initiation* of a nomadic phase center around the *callosus* brood, with the larval brood then a minor factor. Furthermore, I have never advocated for this process a telic concept such as an “appel” from brood, but in view of the facts have opposed it *qua* “appeal” or “Nahrungsbedürfnis” (14, 22).

It seems clear, then, that the first part of a nomadic phase in *Eciton* and the single emigration of *Anomma* have equivalent essential causes, centering around a massive stimulative effect based upon the eclosion of a mature *pupal* brood.

What about the larval stage? When the nomadic phase begins in *Eciton* the young brood is microlarval, and hence is at best a minor stimulative factor in the early part of this phase (14, 18). Comparably, RAIGNIER and Van BOVEN find larvae a minority in the broods when the single emigrations occur in *A. wilverthi*, evidently not a factor in the causation of colony movement. The larval stimulative effect should not be excluded, however, as a possible factor influencing other colony functions. As for *Eciton*, although the oncoming larval brood seems to be only a minor factor in general colony function early in the nomadic phase, it thereafter introduces a stimulative effect essential to the continuation and normal completion of this phase. Accordingly, the most striking difference is that whereas *Anomma* seems always to have only one emigration at a time, with an eclosion-excitatory factor the essential cause, a colony of *Eciton* carries out a series of nightly emigrations in a distinct phase. How shall we understand this difference?

In both *Anomma* and *Eciton* an eclosion-excitatory factor arouses nomadism. However, in both, this effect evidently runs its main course in a few days, during which it accounts for the excitation of one lengthy emigration in *Anomma* and large raids and emigrations in the first few

days in *Eciton* (22). In *Anomma*, the failure of further emigrations to follow seems attributable to a comparable waning of the eclosion effect. The difference is that in *Eciton*, as the eclosion-excitatory factor drops in its intensity, an equivalent brood-excitatory factor attains sufficient intensity to replace it as the essential cause of nomadism. This is a growing excitatory effect from the larval brood, which first overlaps the eclosion-stimulative effect of the preceding brood and then replaces it in the dominant excitatory role.

All that follows in the continuation of the nomadic phase, maintained by the larval effect to a conclusion when the larval brood matures and is enclosed, is distinctive to *Eciton* but evidently absent in *Anomma*. But for *Anomma*, we cannot exclude the hypothesis of a larval-stimulative factor influencing colony functions such as raiding and the queen's reproductive processes during the inter-emigration interval, although specific evidence for such effects is lacking.

Theoretically, then, a nomadic phase exists in both of these dorylines, initiated in both by a brood-stimulative effect which may be homologous and not merely analogous. To clarify the last point, a further consideration of what causal nexus mediates the effect of reproductive processes upon colony behavior is in order.

Basic control of functional rhythms in Anomma and Eciton. — Two questions are involved: first, how an active brood actually affects colony behavior, and second, what governs the known rhythm of brood production. On the first question, from considerations already raised it seems probable that comparable brood-stimulative effects initiate nomadism in *Anomma* and *Eciton*, through raising the level of colony excitation to the point of emigration (22). In 1938 I concluded for *E. hamatum* that the brood-stimulative factor is a summation or resultant of tactual and chemoceptive actions exerted by callows or by growing larvae upon adults, through their movements, secretory products, and the like. Broadly considered, there appears to be no inconsistency between my concept of the callow-excitatory factor as the agency initiating a nomadic phase in *Eciton* (14) and the conclusion of RAINIER and Van BOVEN, stated as follows:

« Nous pensons donc devoir accepter comme cause des exodes la libération brusque dans la colonie de plusieurs centaines de mille jeunes ouvrières, que par leur réserve énergétique et leur grande activité excitent la colonie au point qu'un déménagement s'ensuit. » (11, p. 241.)

Although the limited evidence for *Anomma* at this stage may recommend general terms such as these, the concept of a brood-stimulative factor presents itself as the leading guide to further investigation of the causal link between reproductive processes and colony function in *Anomma* as in *Eciton*.

The second question concerns what conditions may govern the reproductive rhythms themselves. It is apparent, as suggested earlier, that whatever controls the timing of the distinct regular broods of *Eciton* is in effect the pacemaker of the colony functional cycle (16). RAINIER

and Van Boven say that emigrations do not depend upon external factors, but upon the internal situation of the colony, the physiological rhythm of egg-laying and of the development of the brood. I agree, if it is understood that "external factors" here are physical events such as lunar cycles, and that the "internal situation of the colony" includes all conditions arising through colony function and behavior (14, 22). The nub of the question clearly concerns what governs the time at which the queen delivers her successive great batches of eggs. Is the control of this rhythm actually autonomous to the queen?

In Eciton the queen lays her eggs in distinct lots and always at a definite time of maximal physogastry, midway in the statary phase (9, 14, 16, 19, 22). The interval between physogastric egg-laying episodes in the queen is characteristic of the species and always is very regular, roughly 35-37 days in *E. hamatum* and 33-37 days in *burchelli*. Three alternative hypotheses present themselves to account for the specific control of this rhythm: 1) physical factors in the extra-colony environment, 2) an independent pace-setter or "endogenous timing mechanism" autonomous to the queen, and 3) a constellation of factors operating on the queen from the colony functional situation. Hypothesis "1" is doubtful on circumstantial grounds, first, because no Eciton reproductive rhythm coincides with an extrinsic physical rhythm, also because no concurrence of colony rhythms is found (14, 20, 22). The rhythm seems to be controlled within the colony.

Although some years ago I believed that hypotheses 2 and 3 were alternatives (16), evidence favoring the latter has since increased steadily. For one thing, it is unlikely that a strictly endogenous timing mechanism would permit a variation such as occurs when an Eciton sexual brood is produced, when the interval between broods is shortened appreciably in *Eciton* (19, 23). In that case, the change appears directly attributable to a more rapid larval development in the sexual brood than in worker broods, reducing the time schedule of certain brood-stimulative factors controlling the nomadic phase. It is also indicated here that some extrinsic condition in the colony situation affects the queen metabolically sooner than would occur in the presence of a worker brood.

Hypothesis 3 is supported by evidence indicating that the timing of each periodic large-scale ovulation and egg-laying episode in the Eciton queen is governed by a set of conditions normally reintroduced into the colony situation in dependence upon brood development. The queen's rhythm stops when she is kept in captivity even with her colony, hence normal colony processes in the natural situation are essential for the operation of this rhythm. In both *E. hamatum* and *burchelli*, distinct physogastric episodes in the queen evidently result from causes arising in the colony situation as each further brood nears larval maturity. Moreover, preliminary accelerations in the ovulation of immature generations are synchronized at a different time with augmented trophic and stimulative processes in the colony, just prior to the end of a statary phase (9, 20, 22).

In the second case, however, an incipient physogastry and acceleration in oöcyte maturation are cut short by an abrupt change in the colony situation with the eclosion of mature pupae, soon removing the conditions supporting these developments in the queen.

In effect, therefore, a reciprocal relationship of queen and colony, on a trophallactic basis, governs the timing of the queen's rhythm, and hence indirectly controls the times at which brood-stimulative effects may set off the critical reversals of the nomadic and statary phases in colony function. Among numerous intervening variables would be factors influencing the rate of brood development, as for example microclimatic conditions (e.g., temperature) in the bivouac. The latter, however, are held within a limited, species-characteristic range of variation through the effect of various behavioral and physiological processes incident to normal colony function (24). Clearly, the queen's ovulation rhythm is best understood as part of a system of interdependent processes in the nomad-statary functional cycle of the *Eciton* colony.

For the queen of *Anomma wilverthi*, RAIGNIER and Van BOVEN conclude that an intensification of egg-laying occurs each 20-25 days, persisting for about 10 days. The range of variability in the ovulative rhythm of this queen is not clearly established, however, and may turn out to be much greater than the strikingly regular physogastry of the *Eciton* queen (16). In any case, I believe that in principle the reproductive periodicity of the *Anomma dichthadiigyne* may be accounted for on the basis of the theory I have proposed for *Eciton*, in that both the intensifications of ovulation in the *Anomma* queen and the distinct physogastric episodes in the *Eciton* queen are attributable to effective stimulative and trophic conditions reintroduced as successive broods enter specific stages of development. As causes of periodic resurgences in ovulative functions in the *Anomma* queen, attention is thus focussed upon the possible rôle of a mass of larvae predominant in the brood in the statary interval following an emigration, as well as that of nymphs predominant at times of emigration. In this regard, further evidence is needed concerning concurrences in brood development and in the queen's function, as well as between these conditions and variations in colony functions such as intensified raiding and emigration.

Outstanding species differences in *Anomma*, as in *Eciton*, may be understood in the light of this theory. For example, in *Eciton burchelli*, a shorter nomadic phase of greater duration may be attributed to a greater time range in brood development, and to certain bivouac conditions affecting brood development differently as compared with *hamatum*. A somewhat comparable difference may be involved in the *Dorylus* groups, in which the inter-emigration intervals seem to be considerably longer in *nigricans* than in *wilverthi* (11). RAIGNIER and Van BOVEN attribute this difference to the existence of a "physiological" nest temperature in the latter, absent in the deeper nest of the former. In terms of our theory, broods of *A. nigricans*, developing much more slowly in bivouac micro-

climates making for a lower rate of metabolism than in *wilverthi*, would be expected to introduce much less frequently the stimulative and trophic conditions essential for accelerations of ovulation in the queen. Hence massive nymphal eclosions would occur less frequently in *A. nigricans*, and colony emigrations would be correspondingly less frequent than in *wilverthi*. In sum, the interactions of functions in brood, worker population and queen evidently have characteristically different time relations in these two Anomma groups. It is also clear that both of the contrasted Anomma species represent a common pattern, and that each resembles the other much more than either resembles Eciton in its functional system.

SUMMARY DISCUSSION

From the standpoint of modern Systematics, which is directed at an understanding of genetic processes in evolution, it is imperative to investigate what organic characters are crucial to species-characteristic functional adaptations. In this paper certain groups of doryline ants are compared with respect to function and behavior, as a preliminary to discerning what structures and mechanisms are relevant to adaptation in the respective groups.

Certain aspects of function and behavior may be outlined which seem to distinguish all doryline ants, so far as is known. All known dorylines exhibit some degree of colony nomadism, despite secondary differences in the frequency and regularity of emigration. All have occasional stable nests, relatively well sheltered ecologically, in which the colony settles between nomadic intervals. In all, nomadic phases occur, related to the colony excitement level as dependent upon the stimulative effect of active brood. All have a largely or wholly carnivorous diet, supported by mass forays controlled in scope and vigor mainly by brood-stimulative processes. All colonies are monogynic, possessing wingless queens more or less rhythmic in their reproductive output. All have distinctive wasplike males, characterizing a unique pattern of colony division and mating.

The doryline pattern may be considered the product of interrelated functional properties common to the workers, the queen, and to the brood in each species. Essential to the species pattern are general characteristics of the workers. These include properties of secretion and sensitivity permitting the laying down of chemical traces and the utilization of these in foraging. Orientation thus has a non-visual, contact-chemical basis. This condition, together with other properties, facilitates an intimate integration in group activities, marked by communicative processes termed *pressure* and *drainage*. Such properties, together with others influencing action, account for a characteristic pattern of movement marked, when a forager advances into chemically unsaturated terrain, by a hesitant, meandering advance with flitting, wasplike rotatory antennal

movements, then a quick retreat. A strong group responsiveness is indicated in all species by a proneness to form clusters or masses under stimulative conditions of low intensity and minimal change. Such processes are basic to nesting. Doryline workers manifest at all times a close affinity with and an intimate responsiveness to the brood.

The queen and workers of doryline colonies exhibit a great dependence of metabolism and general function upon the group situation, and upon brood condition in particular. Consistent with this fact, it is likely that the rhythmic variations characterizing the prodigious reproductive functions of the queen are attributable to periodic changes in the colony stimulative and trophic situation centering around condition of the brood. Alternative hypotheses for the queen's rhythm, such as extra-colony physical rhythms, or a timing mechanism strictly endogenous to the queen, seem excluded. Because of a basic dependence of doryline colony function upon the brood, characteristic cyclic variations in foraging and in nomadism arise throughout the subfamily.

How far do these similarities depend upon characters retained from the hypothetical pre-doryline ancestor, and how far upon convergent adaptations? It is probable that the common aspect of cyclic function depends upon characteristics underlying reproduction, development and related processes which are essentially homologous among the dorylines. In the degree to which the significant mechanisms have been modified along secondary lines, striking differences evidently have appeared in the various doryline genera without loss of the basic, cycle-maintaining factors. Certain of these differences have been outlined in this paper, against the background of similarities.

One striking secondary difference among the dorylines is the extent to which the hypogaecic tendency is displayed in the different genera. In contrast to most of the dorylines which are more or less subterranean, particularly in nesting, the Ecitons are dominantly and efficiently adapted to a surface habitat. Through mechanisms promoting a surface adjustment in behavior and in ecology, there has appeared in these army ants the most complex and precisely organized pattern of colony function in all known dorylines. The nature of these mechanisms has been suggested here, but no doubt greatly over-simplified.

It is probable that the Ecitons may be considered the most specialized of all dorylines, if by specialization we mean the extent to which evolutionary differentiation has progressed along given adaptive lines. But the term "specialization", like "generalization", is relative. Thus RAINIER and Van BOVEN state that the Eciton queen is more generalized than the *Anomma* queen. Presumably their reason is that the driver-ant queen is considerably more prolific than the army-ant queen. But it would seem that greater fecundity, as with any other adaptive character, should be evaluated as to relative specialization in terms of its relationship to other adaptive processes in the colony. This character in the case of *Anomma* seems to be involved in fewer relationships with the general

colony functional pattern than in *Eciton*, and may therefore be considered less specialized than the lower fecundity of the *Eciton* queen.

The *Anomma* pattern is more variable, and evidently less intricate in its internal mechanisms than that of the *Ecitons*. For example, although an eclosion-stimulative effect initiates each further nomadic phase in both groups, its timing seems considerably more regular in *Eciton*. Greater regularity here indicates a more complex system of controls. Furthermore, *Anomma* does not exhibit the larval-stimulative effect in the prominent rôle which in *Eciton* maintains the remainder of a protracted nomadic phase. In this respect, an important factor may be the considerably less regular and less delimited peaks in the reproductive function of the *Anomma* queen, as well as the apparent incapacity of *Anomma* to overlap successive generations as regularly and as precisely as in *Eciton*. Another important matter is the group of factors making *Anomma* hypogaecic.

The adaptation of *Eciton* to a terrestrial life has brought a much more complex and intricately organized functional pattern than that of *Anomma*, with its essentially subterranean adjustment. Thus in the latter the extensive diurnal adaptations are lacking which in *Eciton* divide the nomadic phase into routine daily units of raiding and emigration. Also, the *Eciton* bivouac or temporary nest evidently affords a more stable microclimate contributing to a higher rate of general colony metabolism and more involved brood-colony relationships than in *Anomma*. Furthermore, in *Eciton* the developmental environment may facilitate a more effective convergence of relative growth rates in the polymorphic brood, tending to increase the summative aspects of the brood-stimulative factor over those of *Anomma* at earlier developmental stages. This may be the basis of the absence of a strong larval-stimulative factor underlying nomadism in *Anomma*, though not excluding other larval effects as upon colony raiding, and upon ovulation in the queen. For these striking differences the more stringent selective effect of surface conditions in *Eciton* evolution, in contrast to the simpler, less pressing conditions prevailing in the hypogaecic *Anomma*, may be held largely responsible.

However much the derivatives of the ancestral doryline pattern may have been subjected to the change, addition, or loss of certain elements in the course of convergent evolution, the cycle-maintaining core seems to have persisted in all. The basic part of their functional system may be considered the array of characters concerning queen, workers and brood which admits the doryline type of close reciprocal relationship between reproductive processes and colony operations. Better than any other ant, this entire subfamily has maintained what is apparently its essential ancestral adaptive system with its combination of carnivorous diet and large colonies. What has made this possible should be clarified by further comparative studies of the various doryline subgroups.

CONCLUSIONS

1. Species differences among the doryline ants in the pattern of predatory raiding are based upon differences in characteristic properties of sensitivity, secretion, conduction and action among the workers. Closely related species often differ far more in such respects than species in different genera.

2. Basic similarities among the dorylines, including continentally separated groups, involve cyclic colony functions and emigrations, centering in brood-colony relationships.

3. The first part of a nomadic phase in *Eciton* and the spaced single emigrations in *Anomma* involve homologous reproductive processes as essential causes, expressed as a massive excitatory effect exerted through the eclosion of a mature pupal brood.

4. The interval of the intermittent emigration in *Anomma* is regarded as a *nomadic phase* equivalent to the onset of nomadism in *Eciton*, because the initiation of the nomadic condition has homologous causes in the two cases. Each inter-emigration interval in *Anomma* is due as in *Eciton* to the absence of brood-excitatory factors adequate for nomadism, and is therefore considered a *statory phase*. Consequently, *Anomma* may be said to have an identifiable nomad-statory functional cycle equivalent to that of *Eciton*.

5. The principal difference between the functional patterns of *Anomma* and *Eciton* lies in the fact that fewer internal reverberatory (feed-back) processes are involved in *Anomma*. One striking difference is that although in *Eciton* the energizing effect of a larval brood succeeds that of a nymphal eclosion and maintains a regular nomadic phase to its end, in *Anomma* this specific process is absent and the nomadic phase is abbreviated.

6. Although in *Anomma* no larval-stimulative factor seems to underlie emigration as in *Eciton*, such a factor may be essential in other ways to the colony functional pattern. In the inter-emigration intervals, at times when larvae predominate in the brood, their stimulative and trophic effects may serve to augment raiding, and may also influence the queen's reproductive processes somewhat as in *Eciton*.

7. It is probable that in the dorylines generally the queen's reproductive rhythm is controlled through a set of reciprocal stimulative and trophic relationships with her colony, rather than by a timing mechanism autonomous to the queen.

8. The brood-stimulative processes which are the main determinants of functional changes both in *Eciton* and in *Anomma* involve complex functional interrelationships between brood, queen and worker population. Therefore the timing of the colony functional cycle, determined through these processes, cannot be attributed to any specific 'clock mechanism' in the colony.

9. In the dorylines, species differences in the durations of the stages in brood development, and hence in the control of time relations in the colony functional cycle depend upon an array of factors (from food supply to bivouac temperature) influencing development.

10. The nomad-statory functional cycle characteristic of all known dorylines is attributable to the operation of a system of interdependent processes arising through properties of workers, queen and brood.

11. Characteristics basic to such rhythmic functions evidently have persisted from the common pre-doryline ancestor, and may be considered homologous. Species and generic functional patterns exhibit secondary convergences and divergencies particularly in dependence upon the evolution of secondary hypogaecic or epigaecic adaptations.

12. The complexity and precision of cyclic colony functions in the species of *Eciton*, evidently greatest in the subfamily, are attributed mainly to secondary evolutionary adjustments to an epigaecic, surface life.

Résumé.

Certaines espèces et certains genres de Fourmis dorylines ont été comparés, en ce qui concerne les fonctions des colonies telles que les raids et déménagements, avant de discerner quels sont les caractères qui, pour l'individu et pour le groupe, sont à la base des différents modes d'adaptation. Chez toutes les dorylines, les fonctions de la colonie sont cycliques et elles doivent particulièrement leurs variations temporaires à des changements dans l'état du couvain.

En principe, le phénomène de nomadisme offre une base équivalente chez le genre *Eciton* du Nouveau Monde et chez le genre *Dorylus* du Vieux Monde. Chez ces deux genres, la reprise périodique de la fonction nomadique qui se produit après des intervalles de non-émigration est due spécifiquement à l'effet stimulant massif d'un couvain nymphal arrivant à éclosion. Une différence frappante est que chez *Eciton* la fonction nomadique se poursuit pendant le nombre de jours qui sont caractéristiques de l'espèce et pendant lesquels l'effet stimulant d'un couvain larvaire en croissance provoque des raids quotidiens successifs et importants ainsi que des déménagements nocturnes. Bien que chez *Anomma* l'effet stimulant des larves ne provoque pas directement le nomadisme, il est susceptible de faciliter les raids de la colonie ainsi que les processus de reproduction de la reine, et il exerce ainsi une influence indirecte sur le cycle fonctionnel de la colonie.

Le fait que les fonctions cycliques sont moins régulières chez *Anomma* que chez *Eciton* doit être attribué principalement à l'existence, chez le premier, d'un nombre moindre de phénomènes internes fonctionnels tels que le « feedback ». Et cependant, contrairement à une conclusion de RAGNIER et VAN BOVEN, le système fonctionnel des deux genres peut se comprendre dans le cadre de la théorie de l'auteur sur l'alternance des phases *nomadiques* et *statiques*. Les différences entre genres, ainsi que les différences entre espèces d'un même genre dans le déclenchement et la durée de ces phases successives sont attribuées, dans les divers cas, à des différences dues aux changements de stimulants et aux propriétés trophiques des couvains en développement. Les processus rythmiques de reproduction de la reine ne sont pas ceux qui contrôlent essentiellement le départ et la durée dans le cycle fonctionnel de la colonie, mais ils sont eux-mêmes, quant à leurs fluctuations principales, sous la dépendance des conditions de stimulation et de trophisme dans la colonie, conditions qui sont extrinsèques à la reine et qui dépendent essentiellement de l'état du couvain. Ce principe s'applique aussi bien, en général, à *Eciton* qu'à *Anomma*.

Eciton et *Anomma* diffèrent profondément dans les régimes de leur activité quotidienne, ainsi que dans les phénomènes cycliques de leur vie observés sur une période plus longue. De telles différences sont dues, avant tout, à l'adaptation d'*Eciton* à un habitat de surface pour la nidification, tandis qu'*Anomma* est adaptée à un habitat souterrain pour ce même objet. Le système fonctionnel d'*Eciton*, plus complexe et plus précis, comporte des adaptations à limites plus faibles pour le couvain et les populations de la colonie, adaptations qui permettent des horaires réguliers de jour et de nuit qui manquent chez *Anomma*. A la base de ces différences, l'auteur estime que des facteurs visuels et infracuticulaires, ainsi que les autres caractères des ouvriers, de la reine et du couvain, jouent le rôle principal.

En commençant par une comparaison entre deux espèces d'*Eciton*, la discussion porte sur les caractères tels que ceux qui affectent la croissance relative des individus dans les couvains polymorphiques en rapport avec les causes de fonctionnement de la colonie. Chez *Eciton*, il existe une disparité très nette dans le coefficient relatif de croissance entre les maxima et les minima pour le couvain polymorphique, et c'est suffisant pour permettre d'admettre un très important effet stimulant total du couvain qui est la cause du nomadisme presque dès le début du stade larvaire. Chez *Anomma*, ce caractère paraît si peu marqué que l'effet stimulant larvaire ne saurait intervenir directement en tant que cause du nomadisme. Dans tous les cas, l'effet larvaire chez *Anomma* est très pro-

bablement en cause dans les fonctions cycliques de la colonie, par suite de l'excitation et des effets trophiques qui influencent les raids de la colonie et les fonctions reproductives de la reine.

Chez les dorylines, les différences entre les modes de fonctions des groupes d'espèces et de genres, comme dans le cas des raids, des déménagements et de la formation de nids temporaires, sont fondées sur les propriétés spécifiques individuelles de sensibilité, de neurophysiologie, de sécrétion et de mouvement. Il est particulièrement intéressant d'observer les différences frappantes entre les modes de raids d'espèces d'*Eciton* étroitement apparentées, tandis qu'il existe des similitudes dans le système des groupes prédateurs de genres séparés sur divers continents. Les similitudes fondamentales parmi les groupes de dorylines reposent sur des facteurs qui se rapportent aux rythmes reproductifs et qui contrôlent le cycle fonctionnel. La comparaison des groupes à ces divers points de vue peut, sans doute, aider à comprendre comment des facteurs qui sont à la base des similitudes et des différences de fonctions ont évolué chez les Fourmis dorylines.

Zusammenfassung.

Gewisse Arten und Gattungen von Ameisen der Unterfamilie Dorylinae wurden hinsichtlich der Tätigkeit der Kolonien, wie z. B. Razzias und Auswanderungen, verglichen, um die Eigenschaften zu ermitteln, welche für das Einzelwesen und für die Gruppe den verschiedenen Anpassungsweisen zugrunde liegen. Bei allen Dorylinen sind die Tätigkeiten der Kolonie zyklisch, und ihre zeitlichen Verschiedenheiten hängen hauptsächlich von den Wachstumsveränderungen in der Brut ab.

Im Prinzip beruht der Nomadismus bei der Gattung *Eciton* der Neuen Welt und der Gattung *Dorylus* der Alten Welt auf derselben Grundlage. Bei beiden Gattungen wird die periodische Wiederaufnahme der nomadischen Tätigkeit, die nach Zwischenzeiten ohne Auswanderung erfolgt, durch den massiven Stimulationseffekt des Reifwerdens einer nymphischen Brut ausgelöst. Eine Besonderheit von *Eciton* liegt darin, daß sich die nomadische Tätigkeit während des bezeichnenden Intervalls fortsetzt, in welchem der Stimulationseffekt einer heranwachsenden Larvenbrut aufeinanderfolgende, weite tägliche Razzias und nächtliche Auswanderungen verursacht. Bei *Anomma* andererseits verursacht die stimulierende Wirkung der Larven nicht direkt Nomadismus, doch sie kann sowohl die Razzias der Kolonie als auch den Fortpflanzungsprozess der Königin erleichtern; so übt sie einen indirekten Einfluß auf den funktionellen Zyklus der Kolonie.

Die geringere Regelmäßigkeit der zyklischen Funktionen bei *Anomma* im Vergleich zu *Eciton* ist hauptsächlich auf die geringere Anzahl von inneren Kreislauf-(feed-back)-Prozessen bei *Anomma* zurückzuführen. Abweichend von RAINIER und VAN BOVEN möchte Verfasser jedoch die Funktionsgestalt beider Gattungen im Rahmen seiner Theorie des Wechsels nomadischer und statischer Phasen verstehen. Inter-generische und interspezifische Unterschiede in der Zeitfolge dieser Phasen werden den Wirkungen der wechselnden stimulativen und trophischen Eigenschaften der heranwachsenden Bruten in den verschiedenen Fällen zugeschrieben. Nicht die rhythmischen reproduktiven Prozesse der Königin regeln im Grunde den funktionellen Zyklus der Kolonie, sondern erstere werden selbst in ihren Hauptschwankungen durch stimulative und trophische Verhältnisse der Kolonie reguliert, außerhalb der Königin und im wesentlichen vom Zustand der Brut abhängig. Dieses Prinzip trifft ebenso für *Anomma* zu wie für *Eciton*.

Eciton und *Anomma* sind sowohl in ihrer täglichen Zeiteinteilung als auch in ihrer zyklischen Routine während längerer Zeiträume auffallend verschieden. Solche Unterschiede sind vor allem der Anpassung der *Eciton*-Neste an ein Leben auf der Oberfläche und derer von *Anomma* an ein unterirdisches zuzuschreiben. Die verwickelten und genauen Funktionsgestalten der *Eciton*-arten beruhen hauptsächlich auf Anpassungen, welche Brut und Kolonie in kleineren Grenzen halten und ein regelmäßiges Tag- und

Nacht-Zeitschema ermöglichen, das bei *Anomma* fehlt. Als Grundlage dieser Unterschiede werden Faktoren visueller und infrakutaner Empfindlichkeit, sowie auch andere Eigenschaften der Arbeiter, der Königin und der Brut, ins Treffen geführt.

Ausgehend von einem Vergleich zwischen zwei Ecitonarten, erörtert Verf. Eigenschaften welche die individuellen Wachstumsraten innerhalb polymorpher Bruten zu beeinflussen geeignet sind. Bei *Eciton* besteht eine ausgesprochene Ungleichheit zwischen maxima und minima in verhältnismäßigen Wuchs der polymorphen Brut, und das führt zu einer stark kumulativen Einwirkung der Brut mit Nomadismus von frühen Larvenstadien an als Folge. Bei *Anomma* kann diese Wirkung so verringert sein, daß der stimulative Effekt der Larven nicht direkt Nomadismus auslösen kann. Selbst dann kann bei *Anomma* die Wirkung der Larven indirekt die zyklischen Funktionen der Kolonie mit-herbeiführen, und zwar durch anreizende und trophische Wirkungen, welche die Razzias der Kolonie und die reproduktiven Funktionen der Königin beeinflussen.

Bei den Ameisen der Unterfamilie Dorylinae beruhen Art- und Gattungsunterschiede in den Gruppenfunktionen, wie z. B. Razzias, Auswanderungen und Bau von zeitweiligen Nesten, auf spezifischen individuellen Eigenheiten der Arbeiter hinsichtlich Empfindlichkeit, Neuropsychologie, Absonderung, und Tätigkeit. Besonders interessant sind die auffallenden Unterschiede im System der Razzias zwischen engverwandten Ecitonarten, verglichen mit Ähnlichkeiten in den räuberischen Gruppenmerkmalen zwischen Gattungen verschiedener Kontinente. Die Hauptähnlichkeiten zwischen Gruppen liegen in Faktoren, die auf Reproduktionsrhythmen, die den funktionellen Zyklus regieren, zurückzuführen sind. Vergleichung von Gruppen in diese Hinsicht könnte zum Verständnis der Art und Weise beitragen, auf die sich die den Gleichheiten und Ungleichheiten der Funktionen zugrunde liegenden Faktoren bei diesen Ameisen entwicklungsgeschichtlich herausgebildet haben.

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ÜBER SEKUNDÄRE GESCHLECHTSMERKMALE BEI EINIGEN AMEISENLARVEN

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Bei der vergleichenden morphologischen Untersuchung an den Larven zahlreicher Ameisenarten (1) findet man einzelne Tiere, die in verschiedenen Merkmalen von den meisten Individuen der gleichen Art, bzw. desselben Nestes, abweichen. Die Unterschiede betreffen nurwenige Merkmale. Die übrigen Kennzeichen dagegen lassen keinen Zweifel darüber aufkommen, daß die auffälligen Larven tatsächlich der Art angehören, in deren Nest sie gefunden wurden. Es sind also nicht etwa nahe verwandte Gäste oder Parasiten.

Der Sexualdimorphismus bei Ameisenlarven ist m. W. bisher noch nicht eingehend untersucht worden. Nur nebenbei werden gelegentlich Merkmale erwähnt, die für die Larven einer bestimmten Kaste oder eines Geschlechtes charakteristisch sind. So gibt WHEELER (1935) an, daß sich bei *Allomerus* die reifen Geschlechtslarven durch ihre Größe und Körperform gegenüber den Arbeiterlarven auszeichnen. Schon junge Sexuallarven sind von mehr gedrungenem Körperbau und die Umrißlinie des Rückens erscheint stärker gewölbt, als dies bei den Larven der Arbeiter der Fall ist. Dazu kommt, daß die reifen Geschlechtslarven vor allem durch lange, ventral am Abdomen angeordnete Haare auffallen, die selbst den reifen Arbeiterlarven fehlen. — Die hier beschriebenen Unterschiede beziehen sich also auf die Kaste, nicht auf das Geschlecht der Larven.

Derselbe Forscher (1938) findet bei den männlichen Larven von *Eciton* (*Acamatus*) *schmitti* Em. am Meso- und Metathorax ventrolateral kurze Querlinien oder Gruben, die er als Anlage der Flügel („wing rudiments“) bezeichnet. Sie fehlen den Arbeiterlarven. Die eben erwähnten männlichen Larven lassen am 9. Abdominalsegment Spuren von Gonopoden-Anlagen erkennen, allerdings nur recht schwach. Deutlicher ausgeprägt sind solche Anlagen bei *Eciton hamatum* Fabr., und zwar am 7., 8. und 9. Segment.

Für die männlichen *Dorylus*-Larven führt der gleiche Autor (1943) als kennzeichnend an: „Vorderes Körperteil in einem rechten Winkel nach vorn gebogen; Endsegment einschlankes, konisches Schwänzchen bildend.“ WHEELER G. C. and Jeannette WHEELER (1953) geben einen Überblick über die *Pheidolini*-Larven (Subfam. *Myrmicinae*). Nach ihnen kann man bei *Pheidole* die Larven der einzelnen Kasten, sowie die männlichen und weiblichen Geschlechtslarven an der verschieden ausgebildeten Behaarung erkennen.

Es darf somit als sicher gelten, daß äußerlich erkennbare sekundäre Geschlechtsmerkmale bereits bei den Larven auftreten, zuweilen sogar schon in jugendlichem Alter. Darum besteht die Vermutung zu recht, daß es sich bei den eingangs erwähnten Unterschieden um Larven verschiedenen Geschlechtes handelt.

Für unsere Untersuchungen bieten gerade die beiden Arten *Solenopsis fugax* und

(1) Eine Veröffentlichung der Ergebnisse wird vorbereitet.

Tetramorium caespitum aus der Subfamilie der *Myrmicinae* den Vorteil, daß die erwachsenen Geschlechtslarven die Larven der Arbeiterinnen an Größe weit überragen. Falls die entdeckten Unterschiede geschlechtsgebunden sind, müßten sie also an den großen Sexuallarven am häufigsten auftreten und am deutlichsten ausgeprägt sein. Dies trifft bei den genannten Arten tatsächlich zu. Da die Larven der Arbeiterinnen bei den Ameisen weiblichen Geschlechtes sind, dürften sie den gleichgroßen weiblichen Sexuallarven in morphologischer Hinsicht mehr gleichen als den entsprechenden männlichen Larven. Daß diese Ähnlichkeit nicht bis zu einer völligen Gleichheit zu gehen braucht, hat WHEELER (1935) für *Allomerus* nachgewiesen. Wennes aber Merkmale gibt, die nur dem männlichen Geschlechte zukommen und die auch schon an jungen Larven auftreten, müßte man diese von den übrigen Larven gleicher Größe unterscheiden können. Zugleich müßten sie zahlenmäßig hinter diesen zurückstehen. Beide Vermutungen wurden durch die vorliegenden Untersuchungen voll bestätigt.

Vergleicht man die Larven der apocriten Hymenopteren mit denen anderer holometaboler Insekten, so erscheint der Körperbau der ersteren äußerlich relativ einfach. Spuren von Extremitäten oder andere Körperanhänge finden sich nirselten; lediglich die Behaarung weist bei manchen Familien eine größere Mannigfaltigkeit auf. Die Kopfregion mit den Mundwerkzeugen zeigt dagegen eine reich differenzierte Ausgestaltung, sodaß hier die meisten Merkmale zu finden sind, die für eine vergleichend morphologische Untersuchung eine größere Bedeutung haben.

1. — *SOLENOPSIS FUGAX*

Bei einer eingehenden Untersuchung der Larven von *Solenopsis fugax* fiel auf, daß die Haare der Kopfkapsel nicht bei allen Individuen die gleiche Beschaffenheit zeigten.

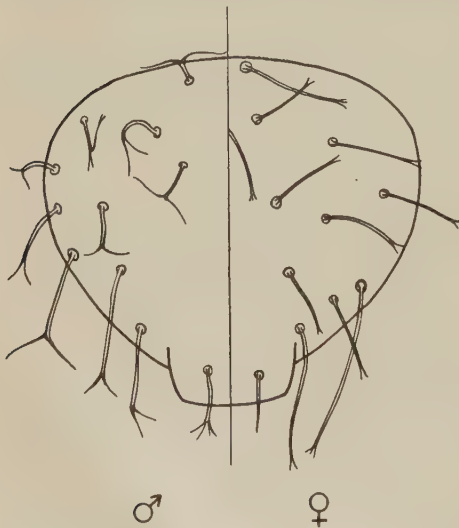


Abb. 1. — *Solenopsis fugax*: Behaarung der Kopfkapsel.

Die Haare auf dem Körper der einzelnen Tiere ließen nur eine verschieden starke Ausbildung erkennen, indem nämlich bei Jung- und Mittellarven (das Stadium der frisch geschlüpften Eilarve blieb außer Betracht) die Behaarung kräftiger und dichter entwickelt ist als bei den Altlarven und Vorpuppen. In diesem letzten Stadium ist bei vielen Arten die Behaarung fast völlig reduziert (etwa bei den *Camponotinae*). Bei *Solenopsis fugax* ist aber selbst an den Vorpuppen noch eine deutlich erkennbare Körperbehaarung vorhanden. Allerdings ließen sich zwischen den beiden Geschlechtern in Bezug auf die Körperhaare keine merklichen Differenzen

nachweisen, die als Unterscheidungsmerkmale in Frage kommen könnten.

Ein völlig anderes Bild ergibt sich aber, wenn wir die Behaarung auf der Kopfkapsel näher betrachten. Die Zahl der Kopfhaare beträgt bei

beiden Geschlechtern 20—25, wozu noch zwei Haare auf dem Clypeus kommen. Die Verteilung der Haare auf dem Kopfe ist weitgehend symmetrisch. Die Länge der Haare erreicht im weiblichen Geschlechte im Durchschnitt etwas größere Werte als im männlichen. Auch sind die weiblichen Kopfhaare (im auffallenden Gegensatz zu den Körperhaaren) fast gar nicht gespalten; lediglich das distale Ende läuft in 2—4 feine Spitzchen aus. Die beiden Haare des Clypeus sind einfach zugespitzt.

Gegenüber dem ♀ und unter sich zeigen die Kopfhaare des ♂ bemerkenswerte Unterschiede. Auf der unteren Hälfte der Kopfkapsel stehen die Haare mehr lateral, sodaß ein zentral gelegener Raum über dem Clypeus frei von Haaren bleibt. Die Haare der oberen Hälfte des Kopfes (Vertex + Frons) gleichen stark den Körperhaaren; sie sind tief dichotom gespalten, wobei die beiden Äste stark divergieren. Zuweilen können diese Äste nochmals dichotom gespalten sein. Die lateral (Gena) entspringenden Haare sind ebenfalls in zwei divergierende Äste gespalten; doch ist hier der gemeinsame Stamm des Haares bedeutend verlängert (Abb. 1). Die beiden Haare des Clypeus laufen in etwa 4 Spitzchen aus.

Ein weiteres gutes Unterscheidungsmerkmal bieten die Mandibeln. Abb. 2 stellt jeweils die rechte Mandibel in Vorderansicht dar. Von Bedeutung ist hier die Ausbildung der Zähne. Während die weibliche Larve außer dem Apicalzahn (Dens incisivus) noch zwei deutliche Nebenzähne (Molares) trägt, wie das für die Larven der Myrmicinen typisch ist, sind diese beim ♂ nicht ausgebildet. Die Mandibel läuft hier distal in eine kurze Spitze aus, zeigt aber nicht die kräftige zahnartige Gestalt wie beim ♀. Zur Mitte hin trägt sie eine Schneide, der — als Rest der nicht ausgebildeten Nebenzähne — ein kleines spitzes Zähnchen aufsitzt.

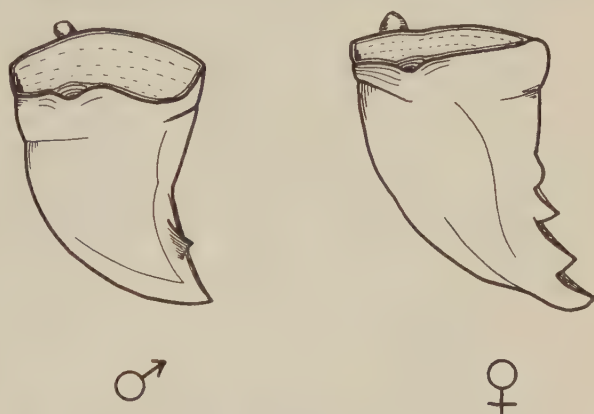


Abb. 2 — *Solenopsis fugax*: Rechte Mandibel in Ansicht von vorne.

2. — *TETRAMORIUM CÆSPITUM*

Von der Körperbehaarung dieser Art gilt zunächst dasselbe, was oben von den *Solenopsis*-Larven gesagt wurde: Auch Altlarven und Vorpuppen tragen noch relativ gut ausgebildete Haare auf dem Körper; doch lassen sie sich hier nach ihrer Form zwei verschiedenen Typen zuordnen (Abb. 3).

Alle Haare sind in ihrer distalen Hälfte stark aufgespalten, wobei eine gewisse Vorliebe für eine mehrfache Dichotomie zu bestehen scheint. Bei der



Abb. 3. — *Tetramorium caespitum*: die beiden verschiedenen Typen der Körperhaare.

Bei der männlichen Larve sind die einzelnen Äste nur wenig divergent, sodaß das ganze Haar etwa einer Pappel mit ihren fast senkrecht aufstrebenden Ästen gleicht. Bei den Haaren des ♀ hingegen zeigen die Äste eine starke Divergenz. Es kommen zwar bei allen Individuen auch vereinzelt Haare vor, die Zwischenformen zwischen den beiden soeben beschriebenen Typen darstellen. Doch ist die weitaus größte Mehrzahl der Haare so deutlich dem einen oder dem andern Typ zugeordnet, daß allein schon an der Beschaffenheit der Körperbehaarung das Geschlecht der Larve festgestellt werden kann.

Noch auffällender wird der Unterschied zwischen den männlichen und den weiblichen Larven, wenn wir die Haare auf dem Kopfe betrachten (Abb. 4). Ihre Zahl beträgt wohl meist 22; die Anordnung ist weitgehend symmetrisch. Der Clypeus trägt auch hier 2 Haare. Es hat wenig Sinn, die Länge der Haare in einem absoluten Maße anzugeben, weil sie selbst beim gleichen Individuum in ziemlich weiten Grenzen schwankt. Beim Vergleich verschiedener Larven fällt aber sofort auf, daß die Haare des ♀ die des ♂ an Länge bedeutend übertreffen, etwa um das Doppelte, wenn wir Durchschnittswerte vergleichen. Was ihre Form betrifft, so finden wir hier wieder zwei verschiedene Typen, die sich aber noch stärker von einander unterscheiden, als dies von den Körperhaaren gilt. Die Kopfhaare der männlichen Larve sind in ihrer distalen Hälfte sehr stark in feinste Spitzchen aufgespalten, sodaß

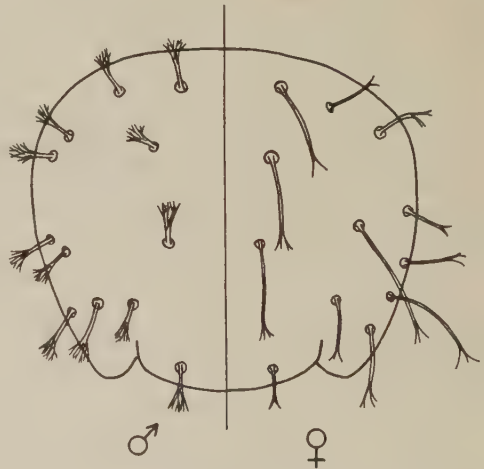


Abb. 4. — *Tetramorium caespitum*: Behaarung der Kopfkapsel.

man sie etwa pinselförmig nennen könnte. Dies trifft auch für die beiden Haare auf dem Clypeus zu. Dagegen sind die Kopfhaare des ♀ fast in ihrer ganzen Länge ungeteilt und laufen erst gegen das Ende hin in 2—4 Spitzen aus. Die beiden Haare auf dem Clypeus sind kurz und nur an der Spitze zweigeteilt.

Schließlich sei noch auf ein Unterscheidungsmerkmal hingewiesen, das allerdings wegen seiner Kleinheit nicht so stark auffällt wie die vorher erwähnten Kennzeichen. Die

Maxillen tragen je einen eingliedrigen kurzen Palpus, der allseitig mit verschiedenartigen Sensillen ausgestattet ist. Distal vom Palpus und nicht weit von ihm entfernt steht die Galea, eigentlich die Außenlade der Maxille. Sie ist jedoch ebenfalls kurz und eingliedrig, ähnlich wie der Palpus, wenn auch meist schlanker und höher als dieser. Die Galea trägt an ihrer Spitze (und nur hier) Sensillen, meist 2 an der Zahl, ist also zu einem Sinnesorgan umgestaltet. Bei *Tetramorium caespitum* läßt sich nun die Form und das gegenseitige Größenverhältnis dieser beiden Sinnesorgane (Palpus und Galea) als unterscheidendes Merkmal für die beiden Geschlechter verwenden. Wie aus der Abb. 5 ersichtlich ist, hat das ♂ einen plump und knollenförmig gestalteten Palpus. Seine Höhe beträgt nur wenig mehr als sein größter Durchmesser, der hier nicht an der Basis liegt, sondern etwas über derselben. Auch die Galea ist breit und plump geformt. Ihre Höhe erreicht nicht ganz die des Palpus. Beim ♀ sind die beiden genannten Organe wesentlich schlanker und schmaler von Gestalt. Besonders gilt dies von der Galea, die zudem den Palpus an Höhe merklich überragt.

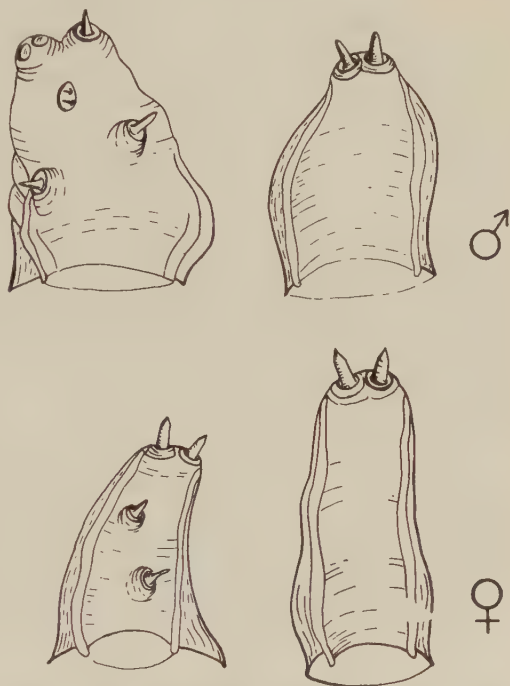


Abb. 5. — *Tetramorium caespitum*: links, *Palpus maxillaris*; rechts, *Galea*.

Wenn es hier gelungen ist, an den Larven zweier Ameisenarten der gleichen Subfamilie (*Myrmicinae*) mit Hilfe sekundärer äußerer Merkmale das Geschlecht bereits an ziemlich frühen Entwicklungsstadien zu erkennen, so besteht die Hoffnung zu recht, daß sich auch bei weiteren Gattungen und Subfamilien brauchbare Erkennungszeichen für die beiden Geschlechter, vielleicht sogar für die beiden verschiedenen Kasten (♀ und ♂) des weiblichen Geschlechtes, auffinden lassen. Die Möglichkeit, das

Geschlecht aller Individuen eines Ameisenvolkes möglichst früh festzustellen, bedeutet eine wertvolle Hilfe, wenn es sich darum handelt, biologische und ökologische Fragen zu klären. Hinsichtlich unserer nützlichen Waldameisen dürfte die frühzeitige Erkennbarkeit des Geschlechtes zudem einige praktische Bedeutung haben.

Summarium.

In larvis, etiam juvenilibus, et præpupis generum *Solenopsis* et *Tetramorium* (Subfam. *Myrmicinae*) genus ex signis secundariis cognosci potest. *Solenopsis fugax* : Mas : Pili e vertice et fronte provenientes (sicut pili per corpus sparsi) in duos ramos divergentes dividuntur ; truncus pili brevior ramis vel etiam æqualis ; pili genæ similes, sed eorum truncus multum largior ; pili clypei ambo cum acumine quadripartito. Mandibula cum brevi acumine ; dentes molares desunt, eorumque locum denticulus acutus tenet. Femina : Pili corporis ut in masculo ; pili capitis omnes longiores, in apice tantum bi- vel tripartiti ; duo pili clypei simplices. Mandibula cum dente incisivo robusto et duobus distinctis molaribus. *Tetramorium cæspitum* : Mas : Pili corporis discissi in multos ramos conflexos ; pili capitis penicillo non dissimiles. Palpus maxillaris crassus et tuberosus. Galea lata, paulo minor quam palpus. Femina : Pili corporis cum ramis expansis ; pili capitis dupli quam in masculo, in apice tantum bi- ad quadripartiti ; pili clypei breves ut in masculo, in apice bifurci. Palpus maxillaris minus crassus. Galea procera, altior quam palpus.

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BEITRAEGE ZUR ANALYSE DER BIENENTAENZE (TEIL I)

von

Wolfgang STECHE

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I. — PROBLEMSTELLUNG

Durch die eingehenden Untersuchungen von K. v. FRISCH, München, ist bekannt, daß die Bienen, die eine gute Tracht gefunden haben im Stock Mitteilungs-„Tänze“ ausführen. Diese enthalten Weisungen über die Entfernung und die Richtung der von ihnen beflogenen Trachtquelle. V. FRISCH konnte eine Kurve aufstellen, welche die Abhängigkeit der *Zahl der Wendungen* eines Tanzes in der Zeiteinheit von der Entfernung des Futterplatzes darstellt. Mit Hilfe dieser Kurve ist es möglich, aus den sogenannten „Schwänzeltänzen“ der Bienen auf der Wabe (s. Abb. 1) annähernd die Entfernung des Futterplatzes zu ermitteln, der vor dem Tanz angeflogen worden war.

In der Durchführung meiner Dissertation: „Gibt es „Dialekte“ der Bienensprache?“ (Zool. Institut, München, 1954; unveröffentlicht) kam ich zu der Beobachtung, daß Flugbienen nach Zurücklegen ein und derselben Flugstrecke bei Darbietung hochkonzentrierter Zuckerlösung schnellere, bei niedriger Konzentration langsamere Tänze ausführen. Die Bienen erhöhten mit zunehmender Konzentration die Zahl der Wendungen pro Zeiteinheit, während sie diese bei niedriger Konzentration entsprechend verringerten. Sie gaben also bei hoher Konzentration der Futterlösung nach v. FRISCH eine geringere Entfernung an als bei weniger guter Zuckerlösung.

TAB. I. — Vergleich der Zahl der Wendungen 15-s von Krainer- und Italienerbienen bei 200 und 500 m Entfernung des Futterplatzes mit 1/2 bzw. 2 mol. Futterlösung.

	200 m.		500 m.	
	1/2 mol.	2 mol.	1/2 mol.	2 mol.
Krainerbienen.	M : 7,6545 σ : 0,7281 n : 102	8,7266 0,7272 111	6,163 0,1217 198	6,833 0,4265 206
	t = 10,74		t = 22,43	
Italienerbienen.	M : 7,0319 σ : 0,6081 n : 135	7,7774 0,7044 90	5,276 0,4247 174	6,1252 0,4645 260
	t = 8,207		t = 21,5	

Dasselbe Phänomen zeigte sich auch bei unterschiedlichen Außentemperaturen. G. ANDERHUBER schreibt dazu folgendes :

„Bei 300 m betrug der Normal-Tanzrhythmus 7, 7 Schwänzler/15 sec, wogegen am 22.9.50 bei 16° Außentemperatur ein Durchschnittswert von 5,8 Schwänzler/15 sec. errechnet wurde.“

Aus diesen Beobachtungen ergibt sich, daß die Anzahl der Wendungen in der Zeiteinheit, aus der wir rückschließend die Entfernung ermitteln, offensichtlich von verschiedenen Faktoren und nicht nur von der Entfernung des Futterplatzes vom Stock bestimmt wird.

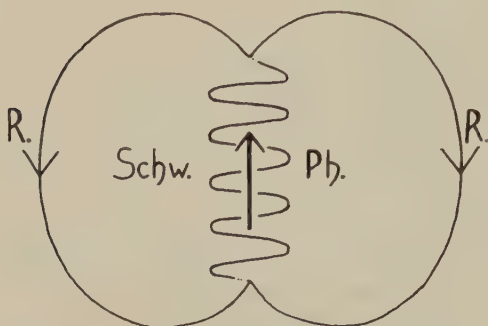


ABB. 1. — Darstellung eines Schwänzeltanzes mit den einzelnen Tanzphasen : Schw. Ph. = Schwänzelphease ; R. = Rücklauf ; Schw. Ph. + R. = « Wendung ».

V. FRISCH schreibt 1948 in der *Oesterr. zool. Zeitschrift* folgendes :

„Die Verlangsamung im Rhythmus der Wendungen geht einher mit einer Verlängerung der geradlinigen Laufstrecke und mit einer Vermehrung der Schwänzelpbewegungen, sodaß der langsamere Tanz nicht an Lebhaftigkeit verliert, ja für das menschliche Empfinden eher an Nachdruck gewinnt. Bei 100 m machen die Tänze mit ihren raschen Wendungen und kurz hingeworfenen Schwänzelpbewegungen einen ausgesprochen hastigen Eindruck. Mit der Mässigung des Tempos bei zunehmender Entfernung

ist es der Schwänzellauf, der immer stärker das Bild beherrscht. Dabei ist die Verlängerung der geradlinigen Laufstrecke nicht bedeutend. Während sie bei Entfernungen von 100—200 m über etwa 1—2 Zellendurchmesser geht, erstreckt sie sich bei 400 m über etwa 2—3 Zellen und bei 1 000 m über etwa 3—4 Zellen. Doch werden diese Abstände nicht streng eingehalten. Regelmässiger scheint mit die Zahl der Schwänzelpbewegungen bei jedem Geradelauf mit zunehmender Entfernung anzuwachsen. Nur kann man sie bei der Schnelligkeit des Vorganges nicht zuverlässig zählen. Ob es für die Wahrnehmung der Bienen mehr auf die Verlangsamung der Wendungen oder auf die Vermehrung der Schwänzelpbewegungen ankommt, weiß ich nicht. Für uns ist ohne besondere Hilfsmittel nur die erstere zu erkennen.“

Bei der Beobachtung der Schwänzeltänze war mir immer wieder aufgefallen, daß Bienen ihren Tanz zur Abgabe des eingetragenen Nektars an andere Stockbienen, oder aus anderen Anlässen, vorwiegend in der „Rücklaufphase“ (s. Abb. 1) unterbrechen.

Eine Unterbrechung der „Schwänzelphease“ habe ich dagegen nur bei offensichtlicher Störung der Tänzerin durch andere Bienen beobachten können. Schon diese Tatsache legt es nahe, daß entscheidende Mitteilungen über die Flugstrecke in der Schwänzelphease selbst enthalten sein müssen. In dieser Annahme wurde ich noch bestärkt durch die recht häufige Beobachtung, daß die Tänzerinnen „Schwänzelpphasen“ tanzen ohne die dazugehörigen Rückläufe und somit Wendungen. Es galt also, die v. FRISCH vermißten „besonderen Hilfsmittel“ zu finden, um die Schwänzelphease genau analysieren zu können. Ich versuchte in München zunächst, bereits existierende Zeitlupenaufnahmen von Bientänzen auszuwerten. Das vorhandene Material reichte jedoch nicht aus, um zu klaren Erkenntnissen kommen zu können. In Zusammenarbeit mit dem Studenten der Physik H. ESCH wurde 1954-1955 am Institut für Bienenkunde der Universität Bonn nachfolgende Methode entwickelt.

II. — METHODIK (1)

Die Messung der Schwänzelsbewegungen wurde nach folgendem Verfahren durchgeführt. Den Flugbienen, die auf bestimmte Entfernungen dressiert waren, wurde nach Versuchen mit Magnetstaub (auf Anregung von Prof. Görze) eine ca. 5 mm lange, gebogene und magnetisierte Minutie durch das zweite Abdomensegment gesteckt. Dieser Eingriff ließ sich durchführen, ohne daß dabei die Intersegmentalhaut verletzt wurde. Um eine Verschiebung der Minutie zu unterbinden, haben wir sie zusätzlich durch einen Tropfen Schellacklösung befestigt. Dadurch machte die Minutie jede Schwingung des Bienenkörpers mit.

Das Versuchsvolk befand sich in einem Zweiwabenbeobachtungsstock nach v. FRISCH. (Die Versuche wurden mit „Krainerbienen“ durchgeführt.) Über die im Stock tanzende Biene hielten wir (außerhalb der Glasscheibe) eine Spule mit hoher Windungszahl. Der durch den Magneten auf der Tänzerin in der Spule entstehende Induktionsstrom wurde über einen Verstärker zunächst auf einen Kathodenstrahl-Oscillographen, später auf einen Schleifen-Oscillographen übertragen. So konnte jede

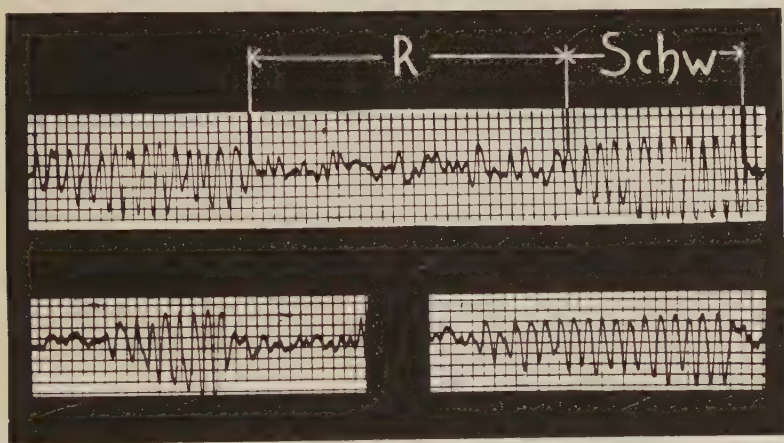


Abb. 2. — Oscillogramme von Tänzen, welche Bienen nach Zurücklegen von 300 m (oben), 200 bez. w. 1 000 m (unten) Flugstrecke ausgeführt haben. (Unter Flugstrecke ist die Entfernung zwischen Beobachtungsstock und Futterplatz zu verstehen.) Schw. — Schwänzelsbewegung; R. = Rücklaufphase.

von der Biene ausgeführte Bewegung aufgezeichnet werden. Die Größe der von dem Oscillographen aufgezeichneten Amplituden war bedingt durch 1 : Die Magnetkraft der Minutie, 2 : den Abstand der Spule von der tanzenden Biene. Da diese beiden Voraussetzungen nicht immer gleich waren, ist eine exakte Auswertung der Amplituden nicht möglich.

(1) Die Durchführung der Versuche wurde finanziert durch die DFG, Herrn Prof. v. FRISCH, der ihm zur Verfügung gestellte Gelder der ROCKEFELLER-STIFTUNG bereitstellte und durch das INSTITUT F. BIENENKUNDE DER UNIVERSITÄT, BONN.

Herrn Prof. GOETZE, der die Versuche mit Rat und Tat großzügig unterstützte, bin ich zu größtem Dank verpflichtet. Ferner gilt mein besonderer Dank Fräulein G. ARMBRUSTER, die bei diesen Versuchen in unermüdlichem Einsatz half. Ebenso möchte ich dem Leiter des physikalischen Instituts der Universität Bonn, Prof. PAUL und seinem Assistenten Dr. ALTHOFF meinen Dank aussprechen.

III. — DIE DURCH DIE MESSUNGEN GEWONNENEN ERGEBNISSE (1)

Wie aus Abb. 2 ersichtlich, ist eine Abgrenzung zwischen Schwänzelpphase und Rücklaufphase im Oscillogramm in der Regel möglich. (Aufzeichnungen, bei denen diese Grenzen gestört waren, wurden nicht ausgewertet.) Der Schleifenscillograph war mit einem Zeitgeber (1/20. Sek.) versehen, sodaß die Bewegungen im Zeitablauf berechnet werden konnten.

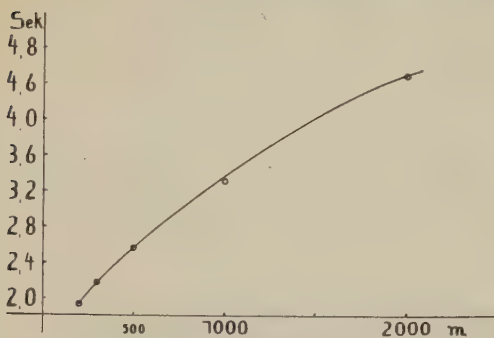


ABB. 3. — Die Dauer der « Wendungen » = W_t in Tänzen, welche Bienen nach Zurücklegen verschiedener Flugstrecken ausgeführt haben.

Zurücklegen bestimmter Flugstrecken an. Sie stellt die reziproke Kurve zu der v. FRISCH aufgestellten Kurve : Wendungen pro 15 Sek. dar.

b) Die Dauer der „Schwänzelpphase“ = S_t . — Hier ist die Zeitdauer der Schwänzelpphase gesondert herausgegriffen. Die öfters unterbrochenen Rückläufe sind also nicht mit in die Messung einbezogen.

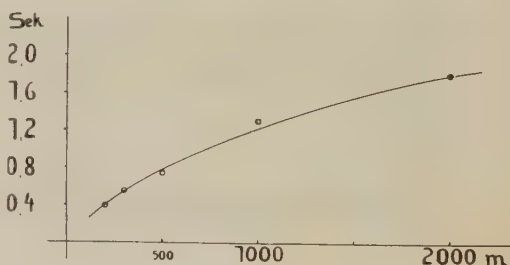


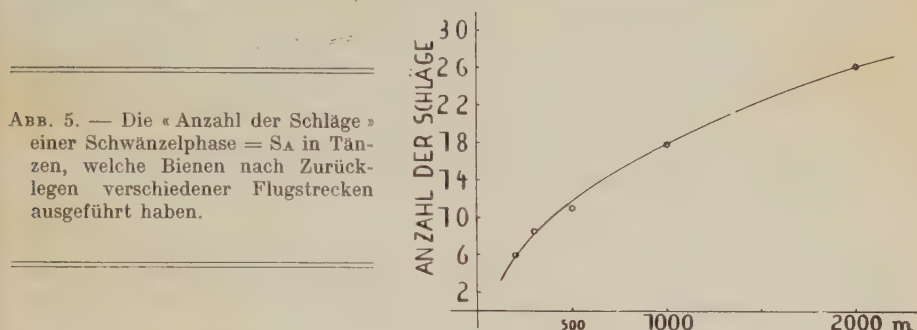
ABB. 4. — Die Dauer der « Schwänzelpphase » = S_t in Tänzen, welche Bienen nach Zurücklegen verschiedener Flugstrecken ausgeführt haben.

c) Die absolute „Anzahl der Schläge“ pro Schwänzelpphase = S_A . — Wie die Abb. 2 zeigt, sind die Schwingungen in der Zeiteinheit bei sauberen Tänzen stets sinusförmig gestaltet.

Aus $\frac{S_A}{S_t}$ läßt sich die „Frequenz“ = ν errechnen, mit der die Schwin-

(1) Sowohl die Methodik als auch die hier kurz aufgezeigten Ergebnisse wurden durch den Stud. der Physik H. Esch, der am Institut f. Bienenkunde der Universität Bonn als freiwillige Hilfskraft gegen Honorierung eingestellt war und mir bei meinen Versuchen zur Seite stand, in zwei Veröffentlichungen bekannt gegeben. Diese Veröffentlichungen erfolgten ohne mein Wissen und ohne die Einwilligung des Institutsleiters.

gungen in der Schwänzelphase ablaufen. Sie liegt bei den durchgeführten Versuchen im Mittel bei 15,02 Hz.



TAB. II. — Die Streuung der Frequenz der Schwingungen in Tänzen, welche Bienen nach Zurücklegen verschiedener Flugstrecken ausgeführt haben. Bei der Berechnung der erhaltenen Werte fiel auf, daß die Streuung der Frequenz außerordentlich stabil ist.

ENTFERNUNG.	<i>n</i>	<i>M</i> ± STREUUNG.
200 m	29	15,10 ± 0,453
300 m	31	15,52 ± 0,666
500 m	41	15,18 ± 0,453
1 000 m	18	14 ± 0,451
2 000 m	22	14,73 ± 0,445

d) Die „relative Grösse“ der Amplitude ist bei sauberen Tänzen stets annähernd gleichgroß (s. Abb. 2). Eine gesetzmäßig verlaufende Zu- oder Abnahme der Amplitudengröße innerhalb einer Schwänzelphase konnte ich nicht feststellen.

TAB. III. — Die Grösse und Streuung der ermittelten Werte W_t , S_t und S_A aus Tänzen, welche Bienen nach Zurücklegen verschiedener Flugstrecken ausgeführt haben.

ENTFERNUNG.	<i>n</i>	W_t	S_t	S_A
200 m	29	1,930 ± 0,063	0,389 ± 0,0256	5,88 ± 0,337
300 m	31	2,1782 ± 0,118	0,55 ± 0,0476	8,55 ± 0,76
500 m	41	2,56 ± 0,147	0,736 ± 0,066	10,88 ± 0,755
1 000 m	18	3,3 ± 0,155	1,286 ± 0,0827	17,9 ± 0,9
2 000 m	22	4,484 ± 0,262	1,789 ± 0,146	26,3 ± 2,22

IV. — DIE BEDEUTUNG DER „ANZAHL DER SCHLAGE“ IN DER SCHWAENZELPHASE = S_A FUER DIE MITTEILUNG DER FLUGSTRECKE

In Kleinaltendorf bei Meckenheim dressierten wir Bienen an zwei 500 m entfernte Futterplätze, die in entgegengesetzter Richtung aufgestellt und mit starken, verschiedenen Duften versehen waren. Während

der Messungen blieb die Geschwindigkeit des aus wechselnden Richtungen kommenden Windes unter 1 m/sec. Die Futterplätze waren mit Zuckerlösungen von 17,5 bez. w. 65 % versehen. Es wurden abwechselnd Tänze von Bienen der beiden Futterplätze aufgenommen. Die klimatischen Voraussetzungen können also keinen Einfluß auf die Ergebnisse ausgeübt haben. Die Auswertung der Oscillogramme ergab, daß zwischen der Zahl der Schläge von den Bienen der beiden Futterplätze kein signifikanter Unterschied besteht. Die Differenz betrug 0,4 Schläge.

Im Gegensatz dazu zeigte sich in der Frequenz der Schwänzelpase ein statistisch sicherbarer Unterschied. Die den guten Futterplatz befliegenden Sammelbienen tanzten mit einer Frequenz von 18,4 Hz, die den schlechten befliegenden mit nur 14,4 Hz. (bei insgesamt 48 Messungen ist $t = 5,83$).

Auf Grund verschiedener Zusammenhänge, die ich hier nicht im einzelnen ausführen möchte, kann ich die Vermutung äußern, daß auch die Anzahl der Schläge Schwankungen unterworfen ist, die aber gesetzmäßig und zwar parallel zu den von M. LINDAUER ermittelten „Grenzwerten“ im Jahresablauf verlaufen. Diese „Grenzwerte“ stellen die Konzentrationshöhe der Futterlösung dar, die zur Auslösung von Tänzen mindestens vorhanden sein muß.

Durch den Versuch in Kleinaltdorf ist gezeigt, daß die Anzahl der Schläge unabhängig ist von der Höhe der Konzentration des gebotenen Futters, die Frequenz der Schläge aber durch die Qualität des Futters gesetzmässigen Änderungen unterworfen ist.

Die Anzahl der Schläge ist also eine durch äußere Umstände nicht veränderliche Größe, die in fester Beziehung zu einer bestimmten Größe der Flugstrecke steht.

Diese Tatsache läßt mit Sicherheit darauf schliessen, daß die *Entfernungsmittelung im Tanz der Bienen in der Anzahl der Schläge pro Schwänzelpase* enthalten sein muß.

Ueber welche Sinnesorgane die tanzverfolgenden Bienen die Anzahl der Schläge wahrnehmen, kann ich vorläufig noch nicht sagen. Da die nachlaufenden Bienen die Tänzerin stets eifrig mit den Fühlern betasten, ist die Annahme naheliegend, daß durch Summation der durch die Fühler ertasteten einzelnen Schläge ein entsprechend großer Reiz zustande kommt. Eine Wahrnehmung in dieser Form erscheint mir eher möglich als ein Erfassen von ganzen Wendungen in bestimmten Zeiteinheiten.

Für diese Annahme spricht auch die Tatsache, daß wir bei Bienen eine Tanzform beobachten können, das sog. „Rütteln“, bei der keinerlei Wendungen vorkommen, sehr wohl aber charakteristische Schwingungen des Abdomens, in diesem Falle dorsal-ventral. Dafür spricht fernerhin, daß nach Untersuchungen von LINDAUER bei „primitiven“ soziallebenden Hymenopteren eine Alarmierung allein durch starke Vibrationen der Tiere im Lauf auf der Wabe möglich ist, ohne daß irgendwelche Wendungen in charakteristischen Tanzformen vorkommen.

Schließlich ist noch ein Hinweis für die Bedeutung der Schwänzelpase

in einem Versuch von mir enthalten, in dem es gelang, Stockbienen durch den Tanz einer „Attrappe“ zum Ausflug anzuregen. Die Attrappe wurde geradlinig, also ohne jede Wendungen von Hand gelenkt. Sie führte dabei in bestimmten Zeitintervallen, die in etwa dem Rhythmus der Wendungen entsprachen, jeweils eine bestimmte Anzahl von Schlägen in ein und derselben Frequenz aus.

Ueber diese Versuche, die noch erweitert werden sollen, will ich in einer gesonderten Veröffentlichung zusammenfassend berichten.

V. — DER ZUSAMMENHANG ZWISCHEN DER FREQUENZ DER SCHWÄNZELPHASE UND DEM VORAUSGEGANGENEN TRACHTFLUG

a) Im vorigen Abschnitt ist gezeigt, daß bei ein und derselben Flugstrecke die Dauer der Schwänzelphase unterschiedlich sein kann. Bei hohem Zuckergehalt der Futterlösung ist sie relativ kurz, bei geringem Zuckergehalt entsprechend länger. Da die Anzahl der Schläge in beiden Fällen die gleiche ist, wird somit die Frequenz bei hochkonzentrierter Futterlösung beschleunigt, bei niederkonzentrierter Lösung verringert, denn die Frequenz ergibt sich aus $\frac{S_A}{S_t}$

Die Schwänzelzeit S_t , bzw. die Frequenz unterliegt also Schwankungen, die in gesetzmäßiger Abhängigkeit von der Qualität der gebotenen Futterlösung stehen.

V. FRISCH und LINDAUER haben in ihrer Arbeit: „über die Fluggeschwindigkeit der Bienen und über ihre Richtungsweisung bei Seitenwind“ den Beweis erbracht, daß bei gleicher Flugstrecke die Dauer des Fluges der Bienen zum Futterplatz ebenfalls Schwankungen unterliegt, die in gesetzmäßiger Abhängigkeit zu der gebotenen Futterlösung stehen. Bei diesen Versuchen war die Flugstrecke die unveränderliche Größe.

Die Parallelität dieser beiden hier geschilderten Beobachtungen macht es naheliegend, den gesetzmäßigen Zusammenhang zwischen dem Trachtflug und dem darauf folgenden Tanze mathematisch darzustellen. Der Vergleich von Flugstrecke = F_w und Flugzeit (v. Stock zum Futterplatz) = F_t einerseits und der Anzahl der Schläge S_A und der Dauer der Schwänzelphase S_t andererseits führte zu folgendem Ergebnis.

Wenn ich für den Flug zum Futterplatz eine durchschnittliche Fluggeschwindigkeit von 7,4 m/sec = 26,7 km/h voraussetze, was bei der gereichten Futterkonzentration von 65 % nach den Untersuchungen v. FRISCHS und LINDAUERS relativ langsam ist (das Gewicht und der Luftwiderstand der Minutie müssen ja aber zwangsläufig eine Minderung der Fluggeschwindigkeit herbeiführen) so läßt sich folgende Gleichung aufstellen:

$$\text{Frequenz} = \frac{\text{Anzahl der Schläge}}{\text{Dauer der Schwänzelpphase}} = \frac{\text{einfache Flugstrecke,}}{\text{halbe Hinflugzeit}},$$

$$v = \frac{S_A}{S_t} = \frac{F_w}{1/2 F_t}.$$

Wir haben in dieser Gleichung im Zähler jeweils die in fester Korrelation zueinander stehenden unveränderlichen Größen S_A und F_w , im Nenner die variablen Größen S_t und $1/2 F_t$ (1). (In diesem Jahr ist ein Versuch geplant, in dem ich S_A , S_t , F_w und F_t messen will, sodaß alle Werte aus einem Versuch genommen werden können.)

b) Es erhebt sich nun die Frage: wodurch werden die Schwankungen der veränderlichen Variablen $= S_t$ und F_t hervorgerufen?

Im aufgeführten Beispiel waren sie bedingt durch die Konzentration der Zuckerlösung. Bei Fütterung hochkonzentrierter Futterlösung verkürzte sich die Dauer der Schwänzelpphase und der Flugzeit, bei geringerer Konzentration stieg die Dauer beider Werte an. VON FRISCH und LINDAUER interpretierten diese Tatsache durch den Satz: „die größere Eile zur besseren Gaststätte“.

Diese treffende Feststellung kann ich meinerseits dahingehend erweitern: „und die größere Schnelligkeit (höhere Schlagfrequenz) im Werbetanz“.

Können tanzverfolgende Bienen die Unterschiede in der Frequenz der Schläge überhaupt erfassen, und haben diese Schwankungen der Frequenz eine biologische Bedeutung?

Um eine Antwort auf die erste Frage zu erhalten, führte ich eine mechanisch gesteuerte „Bienenattrappe“ durch die auf der Wabe des Beobachtungsstockes sitzenden Bienen. Lag die Frequenz im Bereich um 15 Hz, die wir als durchschnittliche Frequenz in vielen Versuchen ermitteln konnten, so folgten diese interessiert der Attrappe. Wich die Frequenz dagegen stärker von 15 Hz ab, so versuchten die Bienen schnellstens aus dem Bereich der Attrappe zu gelangen, oder sie griffen dieselbe direkt an. (Das gleiche Flüchten zeigt sich auch, wenn Bienen auf der Wabe Zittertänze ausführen. Durch Messungen ist mir bekannt, daß bei Zittertänzen die Frequenz der Schläge teilweise erheblich durcheinandergeraten ist.) Dieser Versuch zeigte, daß die tanzverfolgenden Bienen sehr wohl in der Lage sind, Frequenzunterschiede wahrzunehmen. Da gesteigerte Frequenz gleichbedeutend ist mit guter Tracht, verminderte mit geringer Tracht, können tanzverfolgende Bienen durch Erfassen der Frequenz, Mitteilung über die Qualität, in unserem Falle der Zuckerlösung, erhalten.

Wir wissen aus unzähligen Versuchen, daß mit Zunahme der Konzen-

(1) In der Veröffentlichung v. FRISCH's und LINDAUER's: „Ueber die Fluggeschwindigkeit der Bienen und ihre Richtungsweisung bei Seitenwind“ sind Flugstrecke und Flugzeit genau angegeben. Auf Grund dieser Werte lassen sich mit der oben angeführten Gleichung aus den Mittelwerten Frequenzen von 13—17 Hz. errechnen, die weitgehend den von mir gemessenen Werten entsprechen.

tration der Futterlösung die „Werbekraft“ der Tänze erhöht wird. Je höher die Konzentration der Futterlösung ist, desto mehr Neulinge erscheinen an dem durch den Tanz gemeldeten Futterplatz. Allein diese Tatsache macht es wahrscheinlich, daß wie eben hypothetisch angenommen, die tanzverfolgenden Bienen aus der Frequenz Rückschlüsse auf die Qualität der Zuckerlösung ziehen können.

LINDAUER glaubt dieses Phänomen durch die Funktion der „Abnehmerinnen“ erklären zu können. Er konnte feststellen, daß Trachtbienen, die hochkonzentrierte Lösung eintragen, diese von den Abnehmerinnen sofort abgenommen bekamen. Wenn sie jedoch niederkonzentrierte Lösung in den Stock eintragen, so mußten sie meist die Abnehmerinnen direkt anbetteln, damit diese ihnen die eingetragene Lösung abnahmen. Er konnte zeigen, daß einer schnellen Futterabgabe meistens Tänze folgten, während bei verzögerter Futterabgabe diese oft ausblieben.

Nach seinen Auslegungen ist also die Abgabezeit entscheidend für die Auslösung von Tänzen. Wie wir wissen tanzen aber auch Pollen-eintragende Bienen und Spurbienen eines Schwarmes, die ja keinerlei Futter abgeben. Hier kann die von LINDAUER nachgewiesene Gesetzmäßigkeit also nicht steuernd eingeschaltet gewesen sein. Wenn wir aber wie oben annehmen, daß die Bienen die Schnelligkeit mit der von einer Tänzerin die einzelnen Schläge ausgeführt werden, wahrnehmen können, so ist eine Erklärung dafür gefunden, daß auch bei Pollensammlerinnen und Spurbienen jeweils das beste Angebot bevorzugt aufgesucht wird.

LINDAUER selbst konnte bei seinen großartigen Schwarmuntersuchungen aufzeigen, daß die Tänze der Spurbienen unterschiedliche Werbekraft besitzen. Änderte er die von Spurbienen gefundenen Niststätten in einem für die Bienen positiven Sinne, so gewannen die Tänze auf der Schwarmtraube an Werbekraft. Verschlechterte er sie, z. B. durch Zugluft in der Niststätte, so verloren sie ihre Werbekraft, es kamen keine Neulinge mehr.

Es wäre irrig nach dem bisher Gesagten nun anzunehmen, daß Bienen, die hochkonzentrierte Zuckerlösung eintragen, grundsätzlich „besser“ tanzen als solche, die relativ schlechte in den Stock bringen.

Wie viele Versuche zeigten, brauche ich nur den an einen Futterplatz mit hochkonzentrierter Lösung dressierten Bienen die Aufnahme der Futterlösung durch Zwischenschalten von Fließpapier zu erschweren, sofort läßt die Werbekraft der Tänze nach. Wenn ich aber statt die Aufnahme zu erschweren, der Futterlösung eine winzige Dosis bienengenehmen Duftstoffes hinzufüge, so wird nach kurzer Zeit (die Bienen müssen sich erst an den neuen Duftstoff am Futterplatz gewöhnen) der gegenteilige Effekt eintreten. Die Tänze gewinnen an Werbekraft, obwohl auch dieses Mal die Konzentration der Futterlösung unverändert geblieben ist.

Wir sehen aus diesem und den vorher aufgeführten Beispielen, daß es für Bienen im Ablauf der Handlung (Nektar- und Pollenaufnahme,

Niststätteninspektion) antriebssteigernde bzw. antriebsschwächende Situationen geben muß, die nicht physiologisch bedingt sein können (1). Die „antriebssteigernden Situationen“ (leichte Futteraufnahme, hohe Futterkonzentration, Duft, zugfreie Niststätte, u. a.), durch die die Frequenz im Tanz der Bienen erhöht wird, sind soweit uns bisher bekannt, im Hinblick auf das Volksganze des Bienenstockes stets positiv und nutzbringend.

„Antriebsschwächende Situationen“ sind stets dann gegeben, wenn negative Faktoren im Vollzug der Handlung vorkommen.

Zusammenfassend können wir also feststellen, daß die Tänze der Bienen stets dann mit hoher Frequenz ausgeführt werden, wenn die Tänzerin eine im Hinblick auf das Bienenvolk gute Tracht (ect.) gefunden hat. Im negativen Fälle verringert sich die Frequenz entsprechend.

Bei eigenen Untersuchungen in München kam ich zu der überraschenden Feststellung, daß die Auslösung der Werbetänze von Bienen auch beeinflussbar war durch Tänzerinnen, die für einen anderen Futterplatz

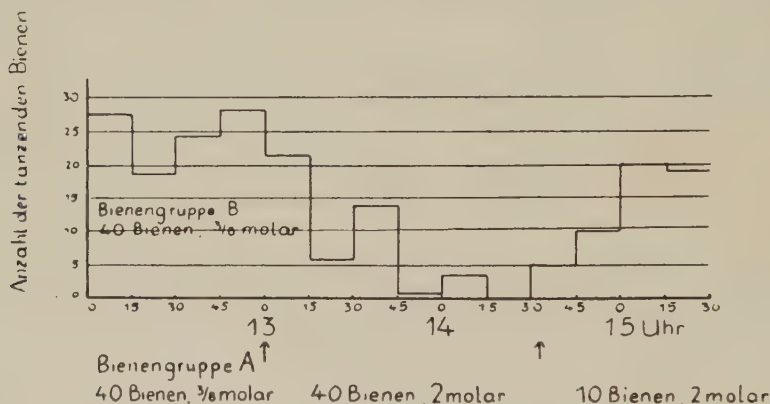


Abb. 6. — Abhängigkeit der Tänze von der Qualität und Quantität des Sammelgutes anderer Sammlergruppen. — Die Kurve gibt die Zahl der Tänze (f. je 15 Min. zusammengefaßt) für eine Gruppe von 40 Bienen (Gruppe B) an, die von 12 bis 15 Uhr mit $\frac{3}{8}$ mol. Zuckerlösung gefüttert wurde. Daneben wurden 40 andere Bienen (Gruppe A) bis 13 Uhr mit $\frac{3}{8}$ dann mit 2 molarer Zuckerlösung gefüttert. Um 14 Uhr 30 wurde ihre Zahl auf 10 Bienen herabgesetzt. (Nach R. BOCH.)

warben. Die Bienen von Futterplatz B bekamen fortlaufend $\frac{3}{8}$ molare Futterlösung gereicht, den Bienen von Futterplatz A wurde abwechselnd $\frac{3}{8}$ bzw. 2 molare Futterlösung geboten.

Wenn die Bienen von A hochkonzentrierte Lösung erhielten, ging die Zahl der Tänze von B zurück, wurde am Futterplatz A niederkonzentrierte Lösung geboten, stieg die Anzahl der Tänze der Bienen von B an.

Die Sammelbienen von B mußten demnach im Stock in Erfahrung

(1) Ich stütze mich hier auf die Begriffsbildung bei E. KRETSCHMER, Abschnitt: „Antriebsfunktionen.“

gebracht haben, daß die Flugbienen von A gleichgutes bzw. schlechteres Futter eintrugen. In Abb. 6 sind Messungen von R. BOCH wiedergegeben, die diese Tatsache klarer als die von mir ermittelten Werte aufzeigen.

Diese Beobachtung macht es wahrscheinlich, daß die im Vollzug der Handlung durch antriebssteigernde bzw. schwächende Situationen zustand kommende Erregung der tanzenden Biene durch das *Zusammen treffen mit anderen Tänzerinnen* im Stock noch *zusätzlich gesteigert* bzw. *gemindert* werden kann. Diese Beeinflußbarkeit der Erregung durch Einflüsse beim Vollzug der Handlung und durch Vorgänge innerhalb des Stockes führen zu der beinahe unwahrscheinlichen Fähigkeit der Bienen, stets *vom vorhandenen Angebot den Bedürfnissen des Stockes entsprechend die optimalen Möglichkeiten auszunutzen*.

Ueber die Wahrnehmung der Frequenzhöhe durch die tanzverfolgende Biene kann ich im Augenblick nur sagen, daß sie, wie der Attrappenversuch es zeigte, möglich ist. Die Annahme ist naheliegend, daß sie über die Chordotonalorgane in den Pedicellen der Fühler erfolgt.

VI. — DISKUSSION

In Kenntnis der geschilderten Zusammenhänge wird jetzt verständlich, wieso die Bienen in den eingangs beschriebenen Versuchen bei gleicher Flugstrecke eine unterschiedliche Zahl von Wendungen in der Zeiteinheit durchliefen.

In einem Falle war durch die verschiedenen Konzentrationen der

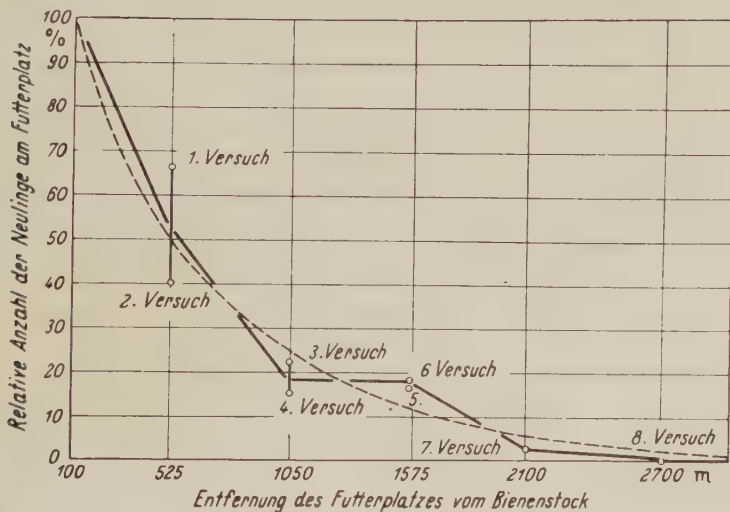


ABB. 7. — Es erscheinen um so weniger neue Sammelbienen am Futterplatz, je weiter er vom Bienenstock entfernt ist. Berechnet auf die gleiche Zahl von Sammelflügen der markierten Bienen, sind die Anzahlen der Neulinge an fernen Futterplätzen in Prozent der am nahen Platz (100 m) erschienen Neulinge angegeben. (N. R. BOCH.)

Futterlösung ein Unterschied der Frequenz und damit der Schwänzelzeiten bedingt, was sich gleichsinnig auf die Wendungszeiten und damit die Zahl der Wendungen pro Zeiteinheit auswirken mußte, da mit einer Änderung der Schwänzelzeiten eine Änderung der Wendungszeiten parallel läuft. Im anderen Falle war die Änderung der Schwänzel- und Wendungszeiten durch den Einfluß der Temperatur bedingt, die, wie wir wissen, ja wesentlich die Schnelligkeit von Bewegungsabläufen beeinflussen kann. In beiden Fällen haben die Tänzerinnen jedoch die richtige Entfernung gewiesen, denn die Zahl der Schläge behielt stets die der Entfernung entsprechende Größe.

Ich möchte annehmen, daß auch mit Vergrößerung der Flugstrecke eine Antriebsminderung (Frequenzerniedrigung) verbunden ist. Dies würde uns erklären, warum bei weit entfernten Futterplätzen die Zahl der anfliegenden „Neulinge“ stark zurückgeht. R. BOCH hat durch eingehende Untersuchungen bewiesen, daß sich mit zunehmender Flugstrecke die Zahl der anfliegenden „Neulinge“ verringert (s. Abb. 7).

Die in Tab. II aufgeführten Mittelwerte der bei verschiedenen Entfernungen gemessenen Frequenzen lassen die Tendenz zu einer Verringerung der Frequenz mit zunehmender Flugweite erkennen.

Wie G. GÖTZE in Wien beim internationalen Bienenzüchter-Kongreß 1956 ausführte, ist die Frequenz der Schläge von ca 15 Hz sicher eine „angeborene“ Komponente, denn sie ist wie W. WITTEKINDT beobachtete, bereits bei Bienen vorhanden, die weder ausgeflogen noch mit Tänzerinnen in Berührung gekommen waren. Die von mir gemessenen Werte zeigen, daß durch antriebssteigernde bzw. -schwächende Situationen die Höhe der Frequenz außerordentlich sinnvoll Schwankungen unterliegt, die jedoch immer um den Grundwert von ca 15 Hz spielen.

Zusammenfassung.

Aus verschiedenen Indizien wird geschlossen, daß in der Schwänzelphase der Bientänze wichtige Komponenten für die Nachrichtenübermittlung enthalten sind. Daher wurde eine Methode entwickelt, die eine genaue Analyse der Bewegungen der Biene in der „Schwänzelphase“ gestattet.

1. Die Versuche erwiesen, daß bei gegebenen Entfernungen stets eine bestimmte „Anzahl von Schlägen“ in der Schwänzelphase auftritt, unabhängig von der Konzentration der Futterlösung und der Temperatur. Diese weitgehende Unabhängigkeit von Außenfaktoren läßt den Schluß zu, daß diese Zahl in enger Anpassung an die Entfernung (Flugweite) reguliert wird, sie sozusagen mitteilt.

2. Die Frequenz, mit der die Schläge ausgeführt werden, liegt im Mittel bei 15 Hz. Durch antriebssteigernde bzw. antriebsschwächende Situationen und durch Begegnungen mit anderen Tänzerinnen im Stock kann die Frequenz gesteigert bzw. verringert werden.

Eine Steigerung der Frequenz ist stets mit Vorgängen verknüpft, die für das gesamte Bienenvolk nutzbringend sind (besonders gute Tracht u. a.). Eine Minderung wird durch negative Faktoren hervorgerufen.

3. Da die Frequenz die „*Lebhaftigkeit*“ des Tanzes bedingt, ist in ihren Schwankungen um den Mittelwert ein Ausdrucksmittel für die Güte der Tracht gegeben.

4. Die *tanzverfolgenden Bienen* können die Höhe der Frequenz offenbar wahrnehmen. Die sogenannten Nachläufer können daher aus den verschiedenen gleichzeitig ausgeführten Tänzen stets diejenigen herausfinden, die ein optimales Trachtangebot anzeigen.

Sommaire.

Plusieurs indices laissent supposer qu'il y a dans la phase frétilante de la danse des abeilles des composantes importantes d'information. Aussi on a développé une méthode qui permet l'analyse exacte des mouvements d'une abeille pendant la « phase frétilante ».

1. Les expériences ont prouvé qu'à une distance déterminée correspond toujours le même *nombre de battements* dans la phase frétilante, indépendant de la concentration du sucre dans la solution et indépendant de la température environnante. Cette indépendance par rapport aux facteurs extérieurs mène à la conclusion que ce nombre est étroitement lié à la distance, que c'est lui qui « communique » le chemin parcouru.

2. La *fréquence* des battements est 15 Hz en moyenne. Par des situations excitant ou apaisant l'impulsion et par les rencontres d'autres danseuses dans la ruche, la fréquence peut être augmentée ou diminuée.

Une augmentation de la fréquence est toujours liée à des événements utiles pour toute la colonie (une miellée excellente et d'autres). Une diminution est causée par des facteurs inverses.

3. Comme la fréquence stipule la *vivacité* de la danse, ses variations autour de la valeur moyenne permettent d'exprimer la qualité de la miellée.

4. Apparemment, les abeilles qui répètent la danse peuvent en apprécier la fréquence. Elles sont capables de choisir celles des danses exercées en même temps qui montrent les conditions les plus favorables quant à la miellée et au besoin de la colonie.

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NOUVELLES DE L'UNION

RÉUNION DE LA SECTION FRANÇAISE

(Samedi 11 mai 1957, Paris).

La réunion se tient au Laboratoire d'Évolution, à 17 heures, devant 20 présents ; 7 membres de la section, empêchés, se sont excusés.

M. le Professeur Grassé préside.

Ordre du jour.

- Préparation du Congrès de juillet ;
- Communication de M. Grassé sur quelques résultats de la Mission Singer-Polignac 1956-1957.

Préparation du Congrès.

M. Richard annonce que 60 personnes sont actuellement inscrites comme membres actifs du Congrès. Il faut ajouter à ce nombre plusieurs personnalités étrangères, qui ont donné leur adhésion provisoire, mais qui n'ont pas encore terminé les dernières formalités d'inscription. Beaucoup de congressistes étrangers seront accompagnés de leurs femmes.

Il est urgent, pour les Français négligents, de donner au plus tôt leur promesse de participation au Congrès. M. Richard relève les noms de chercheurs français qui participeront certainement aux travaux du Congrès et qui, pourtant, n'ont pas retourné leurs fiches d'inscription au Secrétariat.

Actuellement, le Secrétariat est en possession de 30 titres de communications qui se répartissent à peu près également dans les divers groupes de séances.

Devant les propositions reçues et les possibilités de communications proposées, la section française pense que les deux séances de symposia pourront être consacrées à un seul sujet : « Interattraction et effet de groupe chez les Insectes. »

M. Grassé souligne toute l'importance du Congrès qui va se tenir et la valeur des communications prévues. En particulier, il fait remarquer que la participation sera vraiment internationale, puisque nous aurons le plaisir d'accueillir des représentants de toutes les sections déjà constituées et que nous recevrons l'acte de naissance de la section soviétique.

En ce qui concerne la séance prévue d'administration de l'Union, le point le plus important est certainement le renouvellement du Bureau international. Il est évident que la section française, qui a supporté la charge de la première organisation de l'Union, ne peut pas proposer son successeur ; néanmoins, cette question donne lieu à un échange de vues très général entre les présents.

M. Richard demande aux Français de participer nombreux à l'excursion du 11 juillet.

L'excursion dans le Sud-Ouest sera organisée sur le plan matériel par une agence de voyages. Toutefois, les visites de travail à La Rochelle seront placées sous la responsabilité de M. Buchli et de M. Deschamps. M. Grassé accueillera les participants à leur arrivée aux Eyzies. Il s'est assuré les meilleures conditions de visite de la grotte de Lascaux, en particulier.

A la suite de diverses propositions, on prévoit, pendant la durée du Congrès, une exposition de diverses pièces de collection ou de démonstration. M. Noirot est chargé de l'organisation de cette exposition.

Communication de M. Grassé.

M. Grassé expose brièvement quelques-uns des résultats de la récente mission qu'il vient d'effectuer avec M. Noirot en Afrique, sous l'égide de la Fondation Singer-Polignac. Des résultats plus complets seront donnés au cours du Congrès.

NOTE POUR LES AUTEURS

- 1° *Insectes sociaux* publie des mémoires originaux, des notes ou des revues concernant les problèmes relatifs aux insectes sociaux.
- 2° Les auteurs reçoivent gratuitement 50 tirés à part.
- 3° Les manuscrits doivent être adressés à l'un des membres du Comité de rédaction, qui les transmettra au secrétaire.
- 4° Les textes remis pour l'impression doivent être dactylographiés. Leur forme sera considérée comme définitive, et leur étendue ne pourra pas dépasser 20 pages dactylographiées (*), illustration comprise.
- 5° L'illustration des articles est libre. Toutefois le secrétaire se réserve le droit de demander la suppression des figures dont le nombre serait jugé excessif. Les figures au trait sont à la charge de la revue. Les planches, les photographies sont à la charge des auteurs, à l'exception de celles que le secrétaire jugerait pouvoir prendre au compte de la revue. Les documents doivent être fournis prêts à cliquer.
- 6° Les légendes des figures doivent être indépendantes des documents d'illustration.
- 7° Chaque article doit être accompagné d'un sommaire qui en résume les points essentiels. Il sera joint une traduction de ce sommaire en deux autres langues.
- 8° La disposition de la bibliographie doit être conforme aux règles suivantes de présentation :

Date. Nom (prénom). — Titre de l'article (titre du périodique. Année. Numéro du tome, pages de début et de fin de l'article).
- 9° Les épreuves sont adressées aux auteurs pour correction. Elles doivent être retournées SANS DÉLAI au secrétaire : G. Richard, 105, boulevard Raspail, Paris-VI^e (France).

(*) 28 lignes de 67 caractères par page.

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